THE VIRGINIA OPOSSUM IN A TROPICAL DRY FOREST IN COSTA RICA:
FEMALE REPRODUCTIVE STRATEGIES AND
MALE DIMORPHIC CHARACTERS

BY

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I went to the woods because I wished to live deliberately,

to front only the essential facts of life,

and see if I could not learn what it had to teach,

and not, when I came to die, discover that I had not lived.

Henry David Thoreau

"An Opassom hath a head like a Swine, & a taile like a Rat, and is of the Bignes of a Cat. Under her belly shee hath a bagge wherein she lodgeth, carrieth, and sucketh her young"

Captain John Smith, 1612

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THE VIRGINIA OPOSSUM IN A TROPICAL DRY FOREST IN COSTA RICA:
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The Virginia opossum (Didelphis virginiana) has a wide distribution extending from
the temperate climates of southern Canada to the tropics of Costa Rica. Much information
on the life-history pattern of this species exists in North America, but little is known from
Central America. I used live-traps and mark-recapture methods to study a population of
opossums in a tropical dry forest in Costa Rica. I collected data on morphological and
reproductive traits for six months during both 1992 and 1993. Males were significantly
larger than females across the species' range. Sexual dimorphism in body size, canine
length, and sternal glands showed considerable individual variation. These characters may
serve as indicators of a male's dominance, age, or condition, and may be important factors
affecting a male's reproductive success. The morphology of opossums followed a
latitudinal trend predicted by Bergmann's and Allen's Rules of decreasing body size and
increasing tail length from north to south. There was also latitudinal variation in a variety

of reproductive traits. Mean litter size decreased from New York to Florida but increased in Costa Rica. Females in this study first reproduced at six months of age and produced three or four litters during their lifetimes. This contrasts with the usual pattern of two litters in a female's lifetime in North America. To maximize fitness, selection should favor an optimal litter size in a given habitat. If sons and daughters require different amounts of investment, however, there will be a tradeoff between litter size and sex ratio. In this study, a significant inverse correlation was found between the number of offspring and sex ratio: females produced either small, male-biased or large, female-biased litters. Although the tradeoffs between the size and the sex ratio of litters are important factors affecting a female's reproductive success, they are usually considered independently of each other. In addition to between-population or latitudinal variation, this study also revealed considerable within-population variation in life history, morphological, and reproductive characters.

CHAPTER 1
GENERAL INTRODUCTION

The Virginia opossum (<u>Didelphis virginiana</u>) ranges from southern Canada to northwestern Costa Rica. The morphology, genetics, life history, ecology, and behavior have been described and summarized for this species in North America. Although a great deal of information exists for this species in the northern extent of its range, this is not the case for the Virginia opossum in Central America.

This study examined the morphology, female reproductive strategies, and male dimorphic characters of Virginia opossums in a tropical dry forest in Costa Rica. Costa Rica is the southernmost limit of this species' distribution, and these populations should have a morphological and reproductive pattern consistent with the latitudinal gradient found throughout North America. I studied a population of Virginia opossums in Palo Verde National Park, in the northwestern Guanacaste Province of Costa Rica. Live-trapping and mark-recapture methods were used for six months during 1992 and 1993 to examine three main objectives. The first objective was to describe the morphology and reproductive traits of the opossums in Palo Verde and to compare these data with what is known for this species in North America.

In North America, opossums reach a maximum body size in the northern limits of their range and decrease in size in the southern states. This pattern is consistent with Bergmann's Rule that predicts large body size in mammals in northern, colder climates. A large body size has a smaller surface area to volume ratio, and thus, less heat will be lost through the body surface. The opposite pattern is found for body extremities such as ear and tail lengths that increase in size from north to south. Allen's Rule predicts this trend, again on the basis of thermoregulation. There should be selection for shorter ears and tails

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in the north to minimize loss of heat and frost bite, and selection for increasing sizes of extremities in the south to maximize heat radiation through these surfaces. This is the pattern found in the Virginia opossum throughout North America. We do not know whether the populations in Costa Rica follow this trend.

There is also latitudinal variation in the reproductive pattern of opossums. Female opossums reach sexual maturity at six months of age; however, in North America, females generally produce two litters in the year after their birth. Because less than 10% survive to a second reproductive year, female opossums produce an average of two litters during their lifetimes. Reproduction is constrained by the severe winters and heavy snowfall at the northern extremes of their range. The majority of females produce only one litter per year in New York and a maximum of two litters per year in the southern United States. Since the general morphology and several important reproductive traits such as litter size, and the timing and number of litters produced during a year are thought to be affected by severe temperate weather in the northern extreme of the Virginia opossum's range, one might expect a different pattern of reproduction, greater fecundity, and morphological differences for this species in tropical climates. There are no published studies, however, describing the reproductive biology or basic morphology of this species near the southern limits of its range. Therefore, the objectives outlined in Chapter 2 are to quantify the body size differences between the sexes, to describe the population structure and reproductive pattern including the timing and number of litters produced per year, age of first reproduction, and litter size, and finally, to compare the morphological and reproductive traits of this population with data available for this species in the northern distribution of its range.

The second objective of this study was to examine the reproductive pattern found for the opossums in Palo Verde in more detail. Chapter 3 describes the litter size and sex ratio variation among individual females and evaluates female reproductive strategies. To maximize fitness, a female should produce the maximum number of reproducing offspring possible in her lifetime. Under particular ecological circumstances, a female may maximize

her fitness by producing more sons or daughters. If sons and daughters require different amounts of investment, the sex ratio of a female's offspring will affect the overall number of young she can produce. This tradeoff between the size and sex ratio of litters is often not explicitly considered when evaluating female reproductive strategies. Although both the size and the sex ratio of litters are important factors affecting a female's reproductive success, the allocation of energy to reproduction and to male and female function has been considered to be independent of each other and this may not always be the case. This study examines the reproductive strategies of female Virginia opossums by considering natural variation in both the litter size and the sex ratio of offspring produced by female Virginia opossums. The relationship between litter size and the sex ratio is examined, and correlations between these factors and maternal weight, condition, and age are evaluated.

The third objective of this study was to quantify and compare sexually dimorphic characters between the sexes and among males of different age classes. Opossums have several sexually dimorphic characters that show considerable individual variation. There is little information on the extent of variation among males in these characters and their use as indicators of male fitness.

The Virginia opossum has a polygynous mating system and males fight with each other to mate with estrous females. Studies have shown that reproductive success varies greatly among males and that larger males have greater fitness. The morphological differences that may be important in mating have not been examined among male opossums according to age class or during breeding and nonbreeding seasons, yet these dimorphic characters may play an important part in determining a male's reproductive success. Chapter 4 examines body size, canine length, and sternal stains of males during the breeding and nonbreeding seasons. I compare canine size with body size to determine whether these structures are larger than would be expected due to body size differences alone. Finally, I quantify and describe the ontogeny of the sternal stain that is unique

among males. I then evaluate this morphological feature as a possible indicator of male dominance, condition, and age.

Chapter 5 summarizes the major conclusions of this study and offers suggestions for future studies.

CHAPTER 2
LATITUDINAL VARIATION IN THE MORPHOLOGY AND REPRODUCTIVE TRAITS OF THE VIRGINIA OPOSSUM

Introduction

The Virginia opossum (Didelphis virginiana) ranges from southern Canada to northwestern Costa Rica (McManus 1974, Gardner 1982). The morphology, genetics, life history, ecology, and behavior have been described and summarized for this species in North America (McManus 1974, Gardner 1973, 1982, Seidensticker et al. 1987). Although this species demonstrates latitudinal variation in morphology and reproduction, several life-history characteristics of the Virginia opossum remain remarkably consistent throughout its range.

Particular life-history characteristics such as longevity, age at sexual maturity, gestation, and weaning lengths, vary little in this species. In general, the life span of the Virginia opossum is 2 to 2.5 years (Seidensticker et al. 1987, Sunquist and Eisenberg 1993, Wright et al. in press), and female opossums reach sexual maturity at six months of age. The reproductive pattern of the Virginia opossum involves an anestrous period from October to December, followed by mating and production of the first litter in late January or February after a 13 day gestation period (Gardner 1982, Seidensticker et al. 1987). About 90 days are required from birth to weaning.

Within the physiologically-determined timing of particular life-history characteristics, the Virginia opossum may vary in the timing and number of litters produced during a year. In North America females generally produce two litters in the year after their birth (Hartman 1928, Lay 1942, Reynolds 1945, Fitch and Sandidge 1953, Burns and Burns 1957, Gardner 1982, Seidensticker et al. 1987, Sunquist and Eisenberg 1993). Less than 10% of the adult females survive to a second reproductive year (Seidensticker et

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al. 1987, Sunquist and Eisenberg 1993), so female opossums produce an average of two litters in their lifetimes. If the first litter is produced in January or February, the second litter is produced in May or June. This pattern of reproduction has been found from Virginia to Florida (Hartman 1928, Lay 1942, Reynolds 1945, Fitch and Sandidge 1953, Burns and Burns 1957, Gardner 1982, Seidensticker et al. 1987, Sunquist and Eisenberg 1993). In Missouri, however, many females may fail to produce a second litter due to the severity of winter (Reynolds 1945). According to Hossler et al. (1994), only 25% of the female opossums in New York produce two litters in a year, and one litter per year is most common. Due to the long winters and heavy snowfall, production of the first litter does not begin until March and it is difficult to produce and wean a second litter successfully before the onset of the next winter. Therefore, the number of litters produced per year may vary latitudinally in the Virginia opossum, increasing from north to south, however, there is still minimal life-history information for this species in Central America.

Mean litter size also varies latitudinally, with larger litters occurring at the northern extremes of the range (mean = 9.4 in New York vs. 6.6 in Florida; Gardner 1982, Hossler et al. 1994, Sunquist and Eisenberg 1993). Latitudinal variation in life-history traits has often been linked to body size in mammals (Millar and Hickling 1991), however, litter size is often poorly related to body size (Millar 1984). In general, for the Virginia opossum, there are no correlations between female size or weight and litter size within a population (Hartman 1928, Burns and Burns 1957, Seidensticker et al. 1987, Sunquist and Eisenberg 1993, Wright et al. in press), and latitudinal variation in reproductive traits has not been examined in detail throughout the entire range for this species.

Morphological differences include a decrease in body size from north to south, whereas tail length relative to head and body length increases (McManus 1974, Gardner 1982). These morphological trends are consistent with Bergmann's and Allen's rules for latitudinal variation in body size and extremities, respectively (Begon et al. 1986). Bergmann's rule is based on thermoregulatory properties in endotherms and suggests that

since larger body size results in a smaller surface area to volume ratio, this would result in a decrease in heat loss. Therefore, larger body sizes would be expected to occur in northern latitudes with colder climates. Likewise, Allen's rule is based on heat loss through the surface of body extremities and predicts shorter tails and ears in northern latitudes (Begon et al. 1986). Although, a geographic pattern of body size based on the physics of heat exchange has been criticized (McNab 1971, Geist 1987), there is support for the predictions proposed by Bergmann and Allen, and most authors agree that a variety of other factors such as primary productivity, prey availability, rainfall, and seasonality are equally important in shaping mammalian body size (McNab 1971, Barnett 1977, Searcy 1980, Koch 1986, Langvatn and Albon 1986, Seveloff and Boyce 1988, Paterson 1990).

Since the general morphology and several important reproductive traits such as litter size, and the timing and number of litters produced during a year are thought to be affected by severe temperate weather in the northern extreme of the Virginia opossum's range, one might expect a different pattern of reproduction, greater fecundity, and morphological differences for this species in tropical climates. There is some evidence that D. marsupialis can produce three litters in a single year (Fleming 1973, Julien-Laferriere and Atramentowicz 1990). Although this is physiologically possible for the Virginia opossum, there are no published studies describing the reproductive biology or basic morphology of this species near the southern limits of its range. The objectives of this study were to (1) quantify and compare the body size and extremities of male and female Virginia opossums in a tropical dry forest in Costa Rica, (2) describe the population structure and reproductive pattern including the timing and number of litters produced per year, age of first reproduction, and litter size, and (3) compare the morphological and reproductive traits of this population with data available for this species in the northern distribution of its range.

Methods

This study was conducted in Palo Verde National Park (10°21'N, 85°21'W), Guanacaste Province, Costa Rica. Palo Verde contains 19,804 ha of deciduous forest, abandoned pastures, and freshwater marshes bordered by the Tempisque River. The terrestrial habitat is characterized as lowland tropical dry forest (Janzen 1983, Gill 1988). Precipitation is highly seasonal with a six month dry season (Nov-Apr), characterized by strong winds and no precipitation. The six month wet season (May-Oct) receives 1000-1500 mm of rainfall annually (Janzen 1983).

Opossums were captured in Tomahawk live traps from 12 July to 15 September 1991, 1 February to 4 August 1992, and from 20 January to 23 July 1993. Thirty traps were placed 75-100 m apart, forming a grid (300 m x 500 m) that covered a 15 ha area. A total of four grids were established. Traps were set for 4-5 consecutive nights in a grid, then rotated to the next grid for an equal amount of time. All four trapping areas were sampled in this manner for six months each year, three months during the dry season (Jan-Apr) followed by three months during the wet season (May-Aug).

Opossums were processed in the field at the trap site. All adult and subadult opossums were sedated with a mixture of Ketamine and Acepromazine (0.1 cc/kg body wt) and fitted with a numbered ear tag (National Band and Tag Co.) for identification. The animals were weighed and standard morphological measurements were taken including the length of the head and body, ear, and hindfoot. Animals were aged according to molar eruption and tooth wear (Gardner 1982). These date were used to back-date and determine birth dates of all captured subadults and adults.

If females carried pouch young, the offspring were counted and sexed, and head-rump and tail lengths were measured to determine the weight and age of the young (Petrides 1949, Reynolds 1945). The weight of each litter was then subtracted from the female's body weight. Parturition dates were determined by back-dating from the age of

the offspring. All pouch young were toe-clipped for identification. Marked offspring were used to verify the ages of individuals that were aged based on tooth eruption. After the animals were processed, they were returned to the traps and the trap door was wired open. This allowed the opossums to leave the trap after recuperating from the effects of the drugs (1-3 hours). Animals were processed monthly to monitor changes during the study period.

Statistical Analysis

Repeated measures were averaged for individual animals to obtain independent data for each year. For the Palo Verde population, body weights and lengths were compared between the sexes using t-tests. Population structure was compared between the sexes and between years using Chi-square contingency tests. Adult sex ratios were compared to an expected 50:50 ratio using a Chi-square test. Litter sizes were compared between years using Mann Whitney U tests (Abacus Concepts, Statview 1992).

Mean body weight, head and body length, tail length, hindfoot length, and ear length, of both males and females from the Palo Verde population were compared with data from the literature (see Table 2-1) by regressing these variables against latitude (° N). Only studies that specifically gave mean values for the traits considered were used. Mean head and body length was calculated by subtracting mean tail length form mean total length. Significance values were calculated for all regression analyses (Abacus Conscepts, Statview 1992).

Results

Palo Verde Population

The combined 1992 and 1993 trapping seasons resulted in a total of 5,507 trap nights with a total of 1094 opossums captured (256 adults and 838 recaptures). During 1992, 110 adults and 395 pouch young were marked for identification, compared to 146 adults and 431 pouch young in 1993. The adult sex ratio during 1992 equalled 63M:47F; whereas 92M:54F were captured in 1993. Monthly trapping success (total number of animals trapped/total number of traps set) ranged from 8-33% and averaged 20% during the study period.

There was a significant size dimorphism between the sexes; overall males were 28% heavier than females (Table 2-2). Over the entire study period, males averaged 1.78 (± .52) kg compared to 1.29 (± .33) kg for females (t = 8.15, P < .001). Head and body length for males and females averaged 396 (± 45) mm vs. 365 (± 38) mm, respectively (t = 5.67, P < .001). Body extremities (head and body, ear, and hindfoot length) were all significantly larger in males (P < .001). Tail length relative to head and body length was similar for males (92%) and females (93%). Black and white sections of the tail comprised 41% and 51% , respectively, of the pigmented, scaled portion of the tail in both sexes.

Reproductive Pattern

From January to July 1992 and 1993, there were two birth periods (Figs. 2-1a and b). The first birth period of the year began during the first week of February and the second birth period began three months later. A preliminary study during 1991 revealed a third birth period beginning in August (n = 10 females with new pouch young).

During the study period, litter size ranged from 2 to 14 (n = 96). In 1992, mean litter size equalled 7.6 ($\pm$ .31) compared to 8.9 ($\pm$ .27) in 1993. The increase in mean litter size between years was significant (Z = -2.418, P = .02). The mean litter size for both years combined was 8.2.

<u>Population Structure</u>

The population of adult opossums at Palo Verde consisted of four age classes (Figs. 2-2a & b). The youngest age class contained individuals that were six months old at the beginning of the study period (February). These individuals were born in August of the previous year (age class 1). The second and third age classes consisted of individuals that were nine and 12 months old, respectively. These individuals were born during the May and February birth periods of the previous year. The fourth age class contained individuals that were $\geq$ 2 years of age. The age classes in this study refer to adult individuals based on their birth cohort (i.e. February, May, or August). Age classes 1 to 4 in this study correspond to Gardner's (1982) age classes 3 to 6 based on molar eruption and wear.

The population structure differed significantly between years. In 1992, there was no significant difference in the age class distribution of males and females (X^2 = 1.19, P > .10, Fig. 2-2a), and the adult sex ratio was not significantly different from 50:50 (X^2 = 2.05, P > .10). Age classes two and three contained 69% of the adult population. In contrast, the population during 1993 was skewed toward the younger age classes with 63% of the population consisting of individuals from age class one and two. The distribution of the sexes was significantly different (X^2 = 9.81, P < .05; Fig. 2-2b). In addition, the adult sex ratio was significantly male-biased (X^2 = 9.38, P < .01), with the greatest bias occurring in age class three (82% males vs. 18% females, N = 28).

One of the greatest differences in the population structure between years was due to the proportion of individuals in the youngest age class. In 1992, the youngest age class represented only 16% of the adult population. However, during 1993 this age class doubled in size, containing 32% of the population. In both years the oldest age class (individuals entering a second reproductive year) represented less than 20% of the population (15% in 1992 and 18% in 1993). The life span of opossums at Palo Verde ranged from 2 to 2.5 years. This was determined by aging animals that were found dead in the study area (n = 7), and by the timing of the disappearance of age class 4 animals from the trapping grids.

Latitudinal Variation

The data for body weight comparisons ranged from 44 °N to 10 °N latitude. Throughout this range, males were larger than females and the mean body weight of both males and females decreased significantly with decreasing latitude ($R^2 = .69$, P =.003 and $R^2 = .41$, P = .024 for males and females, respectively; Fig. 2-3). From the northern to the southern extremes of this range, mean body size decreased by 50% for males and 46% for females. The pattern was similar for mean head and body length, decreasing north to south by 19% for males and 21% for females, however, the trend was not significant ($R^2 = .01$, P = .829 and $R^2 = .07$, P = .449 for males and females, respectively; Fig 2-4).

The trends in the length of extremities, however, were inconsistent. Mean tail length increased by 20% for males and 15% for females from north to south and the pattern was significant for both sexes ($R^2 = .63$, P = .007 and $R^2 = .41$, P = .026 for males and females respectively, Fig. 2-5). In contrast, there was no significant relationship between mean ear or hindfoot length and latitude (Figs. 2-6 and 2-7, respectively). In fact, the trend was opposite of the trend predicted for body extremities. Mean ear length decreased by 7%

for males and 11% for females from north to south, and mean hindfoot length decreased by 9% for both sexes.

Latitudinal variation in reproductive traits revealed a decrease in mean litter size from 42 °N to 25 °N latitude followed by an increase at 10 °N latitude for the Palo Verde population (Fig. 2-8). Litter size ranged from 1 to 15 and a female's first age of reproduction was 8-9 months of age with the exception of Palo Verde females that began reproducing at six months of age. Females produced two litters per year throughout their range with the exception of a population in New York where 75% of the females produced only one litter/year and in Nicaragua and Costa Rica where females produced three litters/year (Table 2-3). In general, reproduction began in January or February throughout the species' range with the exception of New York where it began later (March).

Discussion

The opossums at Palo Verde had body sizes and tail lengths consistent with the geographic variation found for this species. The Virginia opossum is smaller, has a longer tail and darker body coloration with more distinct facial markings from north to south along its range (Gardner 1973, 1982, McManus 1974, Seidensticker et al. 1987). Body size reaches a maximum in the northernmost populations where males can weigh from 3.5-4.0 kg, whereas females weigh 2.0-2.5 kg (Gardner 1973, 1982). The weights for male and female opossums in this study are most similar to those reported for this species in Nicaragua (1.6 kg for males and 1.2 kg for females; Gardner 1982). The geographic pattern found in the body size of opossums follows Bergmann's rule that predicts larger body sizes in colder climates due to smaller surface area to volume ratios that would reduce heat loss (Begon et al. 1986). The same thermoregulatory mechanism is the basis of Allen's rule that predicts a decrease in extremities (e.g. tail length) in colder climates.

Tail length increases relative to head and body length from north to south in the Virginia opossum. According to Gardner (1973), tail length in the Virginia opossum averages 70% of the head and body length throughout most of North America, increasing to 82% in the southern United States and Central America except for Sonora and Sinoloa, where average tail length reaches 93% of the head and body length. Tail lengths found in this study are consistent with the values described for the Sonoran and Sinoloan populations (Gardner 1973).

The applicability of Bergmann's rule as an explanation for latitudinal trends in mammalian body size has been questioned. Even studies that support Bergmann's rule point out additional factors that may also explain the body size pattern found. Primary productivity and the seasonality of plant resources has been proposed as an important factor influencing body size in many herbivores (Langvatn and Albon 1986, Paterson 1990). The availability of prey and interspecific competitors may also affect body size (McNab 1971). Searcy (1980) suggested a model incorporating size, environmental temperature, and foraging efficiency to predict an "energetically optimum size". In general, there is wide agreement that a variety of factors including thermoregulation may be important in the selection of an optimal body size for a species in a given habitat (McNab 1971, Barnett 1977, Searcy 1980, Koch 1986, Zeveloff and Boyce 1988, Paterson 1990).

The Virginia opossum may conform to the predictions of Bergmann's rule for several reasons. Opossums have sparse fur that does not provide much insulation against the cold, northern climates. Their ears and tails are known to suffer from frost bite in the winter and they will not venture out of their dens if the ambient temperature reaches below -7 °C (Gardner 1982, Seidensticker et al. 1987, Hossler et al. 1994). Therefore, large body size in the northern extremes of the opossum's range may provide some thermoregulatory advantage as well as increasing the ability to store fat to survive periods of food shortage (Searcy 1980). Opossums are opportunistic omnivores foraging primarily on fruits and insects throughout their range (Gardner 1982, Seidensticker et al. 1987), and

their foraging patterns may also be influenced by the effects of temperature and rainfall on primary productivity. Factors such as latitude, coldest monthly average temperature, and mean annual temperature were the best predictors of body size in this species in North America (Koch 1986). Finally, the small body sizes found in opossums at the tropical end of the species' range may also be due to competition with a greater number of generalist foragers that exist in the tropics compared with temperate habitats (McNab 1971, Koch 1986).

Population Structure

The major difference in the population structure of opossums at Palo Verde compared to North American populations is the appearance of four adult age classes compared to three that typically occur in North American populations. This is due to the additional August reproductive bout. In general, there were more adult males than females, which is a pattern found in other studies (Lay 1942, Ryser 1990). This male bias may be due to differential mortality or to the larger home ranges of males (Seidensticker et al. 1987, Ryser 1990) that may allow them to encounter and enter traps more easily.

The distribution of the sexes was significantly different between years and during 1993. This cannot be explained by a trapping bias between years, as the trapping grids and effort were identical both years. The adult population was heavily skewed in favor of males during 1993 (P < .01), perhaps due to dispersal of females from the study area. The lack of females, however, occurs predominantly in the oldest age classes, particularly in age class 3 (Fig. 2-2b). Data from this study indicate that females from this cohort did not differentially disperse out of the study area. Therefore, the disappearance of older females may be due to increased mortality from the expenditure of reproduction.

The presence of many first time breeders during 1993 affected the pattern of reproduction. The extended (2.5 months) birth periods during 1993 were due primarily to

very young (6-month-old) females that came into estrous after the peak birth period and reproduced a month later than the older females. In 1993, the average parturition date during the dry season was week seven and did not differ among older females (9-24 months old). On average, however, six-month-old females reproduced during week eleven. The wet season birth period occurred three months later, and the mean week of parturition was 20 for older females compared to 25 for the youngest females.

Reproduction Pattern

In 1992 reproduction consisted of three birth periods during the year. Each birth period was six weeks long and periods were three months apart. The first birth period occurred in the dry season, beginning in February and ending in mid-March (Fig. 2-1a). The second birth period began in the wet season, extending from the third week of May until the last week of June. A third birth period occurred in August. The August birth peak could be a result of females that failed to find mates or had unsuccessful pregnancies during the May birth period, who then recycled and gave birth later in the year. There are three lines of evidence, however, suggesting that this was not the case, and that a third period of reproduction occurs in August at Palo Verde. First, backdating individuals (subadults) of known age that were captured during 1992 and 1993 indicated a complete cohort of individuals were born in August of the previous year. Second, because all females that were captured during the first two birth periods of the year had pouch young, it seems unlikely that the August births were due to failed pregnancies. Finally, data from a preliminary study from July to September 1991 indicated that females had new pouch young in August, suggesting that after weaning the May cohort, females had another litter in August.

In contrast to the synchronous birth periods of 1992, birth periods were longer in 1993 (Fig. 2-1b). The dry season birth period began the first week of February and

extended into mid-April. The wet season period ranged from the first week of May to mid-July. Female weight at first reproduction averaged 0.60 kg during 1992 and 0.68 kg for 1993. Females began reproducing when they reached sexual maturity at six months of age.

There are three major differences in the reproductive pattern found for the opossums at Palo Verde compared to what has been described for this species in North America. The first difference is the production of three litters in a single year compared to two litters or less per year in North American populations (Table 2-3). Similar to other populations, there was a three month period at the end of the year with no discernible reproduction. In late January and early February mating began, and there were birth peaks in February, May, and August.

Female opossums are physiologically capable of producing three litters per year, but they usually do not attempt a third litter in North America. The offspring born in August would be weaned in November and December, which is the beginning of winter in North America and therefore the young would not be expected to survive. In contrast, data from Nicaragua (Biggers 1966) and Costa Rica (this study) indicate that three litters per year is common. This pattern of increasing breeding opportunites in tropical versus temperate latitudes is common among mammals (Bronson 1989). Studies on Peromyscus spp., lagomorphs, and white-tailed deer, indicate that reproduction is usually restricted to a few months in extreme northern latitudes and, consequently, one litter per year is the norm. In the southern limits of a species' range, the opportunities to breed may extend from six to 12 months a year and the same species may produce several litters during that time (Bronson 1989).

The second major difference in the pattern of reproduction found at Palo Verde compared to North American populations was a female's age of first reproduction. The females born in August of a particular year reach sexual maturity at six months of age, which coincides with the first birth period for this population. During this study, in February, all captured females that were six months and older reproduced. All of these

surviving females also reproduced in May. Although I do not have data following females throughout all three reproductive periods in a year, all of the females trapped during the reproductive periods were pregnant. In addition, the population structure and age distribution of reproductive females indicated that females produced at least three litters in their lifetimes. This contrasts with the pattern of reproduction in North American populations where females forego reproducing in the year of their birth and produce two litters the following year (Hartman 1928, Lay 1942, Reynolds 1945, Fitch and Sandidge 1953, Burns and Burns 1957, Gardner 1982, Seidensticker et al. 1987, Sunquist and Eisenberg 1993; Table 2-3). Usually less than 10% survive to a second reproductive year (Seidensticker et al. 1987, Sunquist and Eisenberg 1993).

The third major difference in the reproductive pattern between North American and Costa Rican populations concerns litter size, which decreases from north to south in North America (Gardner 1982, Seidensticker et al. 1987; Fig. 2-8). The average litter size is 9.4 in New York, (Hossler et al. 1994) decreasing to a mean of 6.3 (Burns and Burns 1957) and 6.6 (Sunquist and Eisenberg 1993) in Florida. The mean litter size of 8.2 for the overall study period at Palo Verde (10 °N) does not follow the trend of decreasing litter size found for other populations in this species. Latitudinal variation in litter size does not follow clear patterns in most mammal species (Millar 1984, Bronson 1989). Most reproductive traits affecting reproductive rate have been linked to body size in mammals (Millar and Hickling 1991), however, body size is a poor predictor of life-history characters in mammals. A decreasing latitudinal trend in litter size has been found in Peromyscus maniculatus (Millar 1989), however, there is large variation at local population levels that is not consistent with this trend (Bronson 1989). The increase in mean litter size found at Palo Verde may be a result of differences in the habitat (e.g. available resources) that enable females to produce larger litters than expected based on latitudinal trends in ambient temperature.

In summary, this study examined a population of the Virginia opossum at the southern limit of the species' range. Male and female body sizes and tail lengths were consistent with those reported for the populations in the southern end of the species' range. Females reproduced when they reached sexual maturity at six months of age. Opossums lived for 2 to 2.5 years and females can typically produce three or four litters during their lifetimes. The additional period of reproduction results in an additional age class present in the adult population.

A female opossum's opportunity to reproduce increases from north to south along the species' range. In North America, at the northern limit of the species' range, females produce, on average, one large litter per year (Hossler et al. 1994). The pattern shifts to two litters per year and mean litter size decreases in the southern populations (Gardner 1982). Since at least 100 days are required from conception to weaning, females can produce a maximum of three litters during a calendar year (Sunquist and Eisenberg 1993). In Palo Verde, females seem to reach the maximum reproductive potential reported for this species by producing three, large litters per year. This may be a result of climatic variables such as ambient temperature and seasonality of rainfall, as well as the availability of resources, that vary among habitats and along latidudinal gradients.

Table 2-1. Literature sources for latitudinal variation in body size and extremities of the Virginia opossum (<u>Didelphis</u> <u>virginiana</u>).

LOCATION	LATITUDE (°N)	SEX	WT (kg)	HB (mm)	TAIL (mm)	FOOT (mm)	EAR (mm)	N	REFERENCES
Pennsylvania	40	M	3.4	488	291	69	54	10	Blumenthal and Kirkland 1976
Pennsylvania	40	F	2.4	464	289	64	55	18	Blumenthal and Kirkland 1976
Ohio	39	F		431	298	63		5	Preble 1942
Arkansas	35	M		414	280	58	49	11	Sealander1979
Arkansas	35	F		387	274	55	49	7	Sealander 1979
Georgia	32	M		306	254	53		6	Golley 1962
Georgia	32	F	1.1	322	261	57		5	Golley 1962
Louisiana	30	M		511	310	62	51	22	Lowery 1974
Louisiana	30	F		430	302	60	50	22	Lowery 1974
Sinoloa/Sonora	27	M		429	376	65	53	8	Gardner1982
Sinoloa/Sonora	27	F		376	389	58	50	8	Gardner1982
Oaxaca	17	M		453	374	65	--	22	Gardner 1982
Oaxaca	17	F		420	358	62	--	18	Gardner 1982
Nicaragua	13	M	1.6	447	377	63	52	20	Gardner 1982
Nicaragua	13	F	1.2	408	352	60	48	20	Gardner 1982
Michigan	44	M	3.6	--	--	--	--	40	Brocke 1970
Michigan	44	F	2.4	--	--	--	--	12	Brocke 1970
New York	42	M	2.8	--	--	--	--	83	Hamilton 1958
New York	42	F	1.9	--	--	--	--	60	Hamilton 1958
Iowa	41	M	3.1	--	--	--	--	5	Wiseman and Hendrickson 1950
Iowa	41	F	1.8	--	--	--	--	10	Pippitt 1976
Illinois	38	M	3.8	--	--	--	--	9	Pippitt 1976
Illinois	38	F	2.4	--	--	--	--	7	Pippitt 1976
Kansas	38	F	1.4	--	--	--	--	18	Fitch and Sandidge 1953
Kansas	38	M	2.9	--	--	--	--	3	Pippitt 1976
Kansas	38	F	2.6	--	--	--	--	4	Pippitt 1976
Louisiana	30	M	2	--	--	--	--	105	Edmunds et al. 1978
Louisiana	30	F	1.8	--	--	--	--	74	Edmunds et al. 1978
Virginia	37	M	2.5	427	302	67	47	163	Seidensticker et al.1987

Table 2-1. Continued.

LOCATION	LATITUDE (°N)	SEX	WT (kg)	HB (mm)	TAIL (mm)	FOOT (mm)	EAR (mm)	N	REFERENCES
Virginia	37	F	1.8	395	300	62	48	90	Seidensticker et al.1987
Mexico	22		2.7	--	--	--	--	--	Gonzalez and Leal 1984
Costa Rica	10	M	1.8	396	363	63	50	150	Marquez1994
Costa Rica	10	F	1.3	365	340	58	49	100	Marquez 1994

Wt = mean body weight
HB = mean head and body length
TL = mean tail length
Foot = mean hindfoot length
Ear = mean ear lenth
-- = data not given in study
N = number of animals measured

Table 2-2. Body size differences between male and female Virginia opossums (Didelphis virginiana) during 1992 and 1993, Palo Verde National Park, Costa Rica.

	Mean Wt (kg)[a]	SD	Mean HB[b]	SD	Mean TL[c]	SD	Mean HF[d]	SD	Mean Ear[e]	SD	N
MALES	1.78	.52	396	45	363	31	68	4	50	4	155
FEMALES	1.29	.33	365	38	340	40	63	4	49	3	100

[a]Differences between the sexes in mean Wt: t = 8.15, P < .001.
[b]HB = Head and body length: t = 5.67, P < .001.
[c]TL = Tail length: t = 5.12, P < .001.
[d]HF = Hindfoot: t = 9.50, P < .001.
[e]Ear: t = 3.78, P < .001.
All measurements in mm.
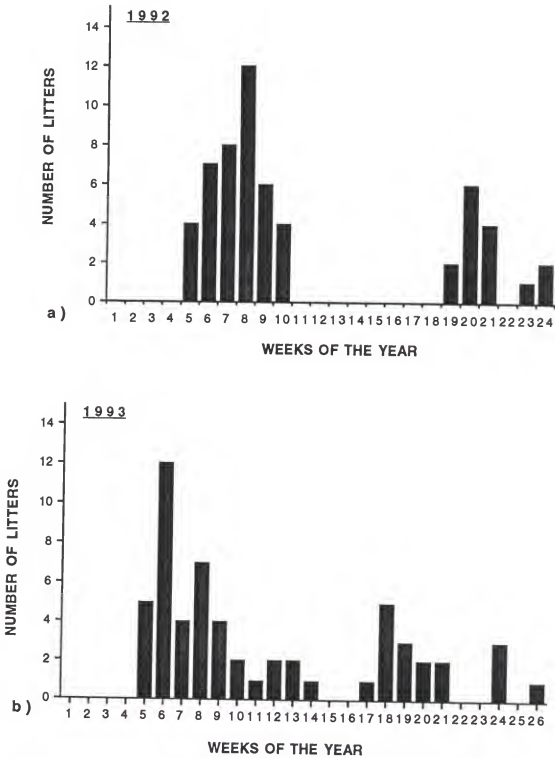
Figure 2-1. Numbers of litters produced by female Virginia opossums (<u>Didelphis</u> <u>virginiana</u>) during the first two birth periods of (a) 1992 and (b) 1993; Palo Verde National Park, Costa Rica.
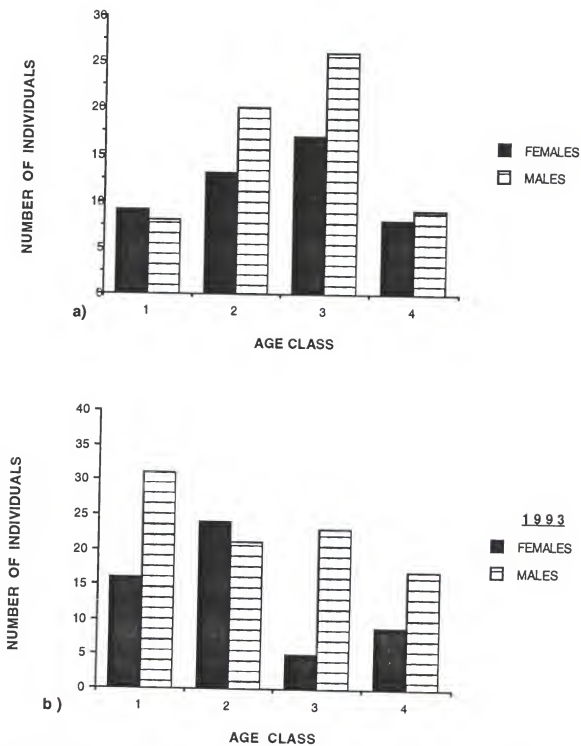
Figure 2-2. Age class distribution of adult male and female Virginia opossums (Didelphis virginiana) in Palo Verde National Park, Costa Rica during (a) 1992 and (b) 1993.
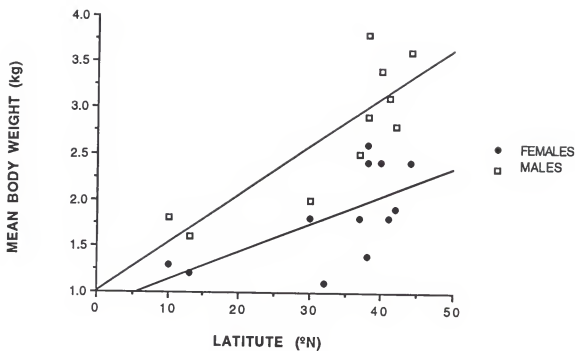
Figure 2-3. Laitudinal variation in the mean body weights of male and female Virginia opossums, $R^2 = .69$, $F = 18.12$, $P = .003$ for males and $R^2 = .41$, $F = 7.07$, $P = .023$ for females. Costa Rica population is at 10 °N. Data are from Table 2-1.
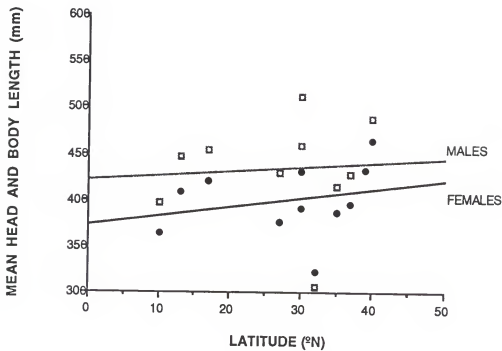
Figure 2-4. Latitudinal variation in mean head and body lengths of male and female Virginia opossums, $R^2 = .01$, $F = .05$, $P = .829$ for males and $R^2 = .07$, $F = .627$, $P = .449$ for females. Costa Rica population is at 10 °N.
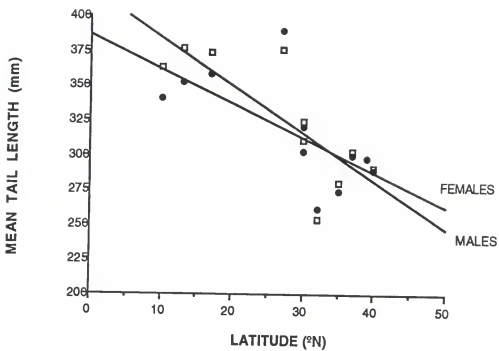
Figure 2-5. Latitudinal variation in mean tail lengths of male and female Virginia opossums, $R^2 = .63$, $F = 13.33$, $P = .007$ for males and $R^2 = .41$, $F = 7.10$, $P = .026$ for females. Costa Rica population is at 10 °N.
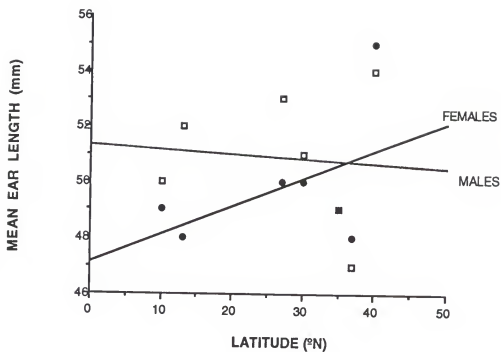
Figure 2-6. Latitudinal variation in mean ear lengths of male and female Virginia opossums, $R^2 = .01$, $F = .03$, $P = .865$ for males and $R^2 = .24$, $F = 1.55$, $P = .269$ for females. Costa Rica population is at 10 $^\circ$N.
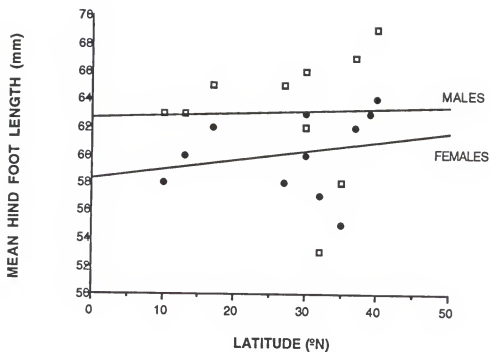
Figure 2-7. Latitudinal variation in mean hindfoot lengths of male and female Virginia opossums, $R^2 = .001$, $F = .01$, $P = .929$ for males and $R^2 = .06$, $F = .57$, $P = .469$ for females. Costa Rica population is at 10 °N.
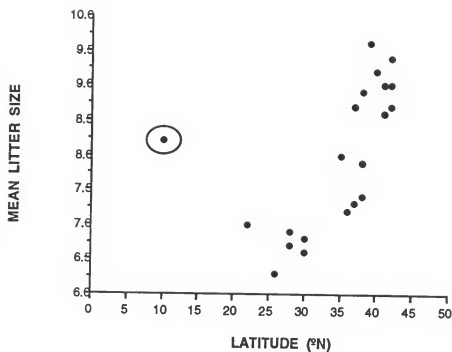
Figure 2-8. Latitudinal variation in mean litter size of Virginia opossums. The circle indicates the overall mean litter size for opossums at Palo Verde National Park, Costa Rica, 1992-1993.

Table 2-3. Summary of the latitudinal variation in reproductive traits of female Virginia opossums throughout their range, including mean litter size, number of litters produced per year, first age of reproduction, and the first month of the breeding season.

LOCATION	LATITUDE (°N)	MEAN LS[a]	MODE	RANGE	N	No.LITTERS/YEAR	AGE[b] (mo)	1st BREED[c]	REFERENCES
New York	42	9	–	1-15	156	–	–	–	VanDruff 1971
New York	42	8.7	9	2-15	346	–	–	–	Hamilton 1958
New York	42	9.4	–	7-14	13	1	9	Mar	Hossie et al. 1994
Iowa	41	9	–	6-12	7	2	–	–	Wiseman and Hendrickson 1950
Nebraska	41	8.6	–	–	23	–	–	–	Wiseman and Hendrickson 1950
Pennsylvania	40	9.2	–	1-14	20	2	–	–	Blumenthal and Kirkland 1976
Pennsylvania	40	–	–	–	–	–	–	–	Biggers 1966
Ohio	40	9.6	–	–	5	2	–	–	Petrides 1949
Missouri	39	8.9	–	5-13	42	2	–	Feb	Reynolds 1945
Illinois	38	7.9	8	–	85	2	–	–	Holmes and Sanderson 1965
Kansas	38	7.4	–	1-12	28	2	9	–	Fitch and Sandidge 1953
Virginia	37	7.3	7	6-9	3	2	–	–	Stout and Sonenshine 1974
Virginia	37	8.7	–	3-15	40	2	9	–	Seidensticker et al. 1987
California	36	7.2	7	4-11	44	–	9	Jan	Reynolds 1952
Arkansas	35	8	–	–	–	2	–	Feb	Sealander and Heidt 1990
Louisiana	30	6.8	–	1-10	68	–	–	–	Edmunds et al. 1978
Texas	30	6.8	–	–	65	2	–	Jan	Lay 1942
Texas	30	6.6	–	–	28	–	–	Jan	Hartman 1928
Florida	28	6.9	–	–	25	2	8	Feb	Sunquist and Eisenberg 1993
Florida	28	6.7	–	–	162	2	8	Feb	Wright et al. in press
Florida	26	6.3	7	3-9	50	2	8	Jan	Burns and Burns 1957
Mexico	22	7	–	–	–	2	8	–	Gonzalez and Leal 1984
Nicaragua	13	–	–	–	–	3	–	–	Gonzalez and Leal 1984
Costa Rica	10	8.2	9	2-14	96	3	6	Feb	Marquez 1994

[a] Mean litter size; [b] First age of reproduction; [c] Onset of the first breeding season of the year, -- = not given in study

CHAPTER 3
REPRODUCTIVE STRATEGIES OF FEMALE OPOSSUMS IN A
TROPICAL DRY FOREST

Introduction

To maximize fitness, a female must allocate energy to produce the maximum number of offspring possible in her lifetime. But a female's fitness depends on the fitness of her offspring. The number of successful offspring a female can produce usually increases with an increase in the size of young (Begon et al. 1986). Large offspring may be more competitive and more successful at obtaining nutrients and dealing with environmental stress. As a female increases her investment in each individual offspring, however, the number she can produce decreases (Smith and Fretwell 1974). This simple relationship between energy and the size and number of offspring becomes more complicated when sons and daughters require different amounts of investment.

Fisher (1930) argued that parents should invest equally in sons and daughters, but if their cost is different, at the end of parental investment, females should bias their litters towards the cheaper sex (Fisher 1930). Under particular ecological circumstances, however, females may increase their fitness by biasing their production of offspring towards the more expensive sex (Trivers and Willard 1973, Werren and Charnov 1978, Charnov 1982, Wright et al. in press). In polygynous mammals, sons are usually the more expensive sex to produce (Clutton-Brock and Albon 1982). If a female could maximize her fitness by producing sons, as a consequence of their increased cost she would produce fewer individuals. Conversely, if a female mammal produced more daughters, she could produce an overall greater number of offspring (Myers 1978). When dealing with organisms that produce large numbers of offspring that differ in their energetic

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requirements, the connection between the number and sex of the offspring must be considered.

The relationship between litter size and the sex ratio (% sons) is often not explicitly considered when evaluating female reproductive strategies (Trivers and Willlard 1973, Clark 1978, Werren and Charnov 1978, Silk 1983, Clutton-Brock and Iason 1986). This may be because litter size has traditionally been considered part of life history evolutionary theory (reproductive effort), whereas the sex ratio of offspring falls under the theories of sex allocation (Charnov 1982, Zhang and Wang 1994). Although both the size and the sex ratio of litters are important factors affecting a female's reproductive success, the allocation of energy to reproduction and to male and female function has been considered to be independent of each other (Zhang and Wang 1994). This may not always be the case.

This study examined the reproductive strategies of female Virginia opossums (Didelphis virginiana) by considering variation in both the litter size and the sex ratio of offspring produced. Female opossums reach sexual maturity at six months of age and may produce a maximum of three or four litters in their life time. In this population there are three birth periods during a year (Feb, May, and Aug). Twenty to 25 young are born after a two week gestation period and crawl unaided into the mother's pouch (Gardner 1982, Seidensticker et al. 1987). Only the individuals that find a functional teat and attach will survive. The number of functional teats usually varies from two to 13. After a two month pouch phase plus a one month nest phase, the young disperse (Gardner 1982, Seidensticker et al. 1987). By this time females are already pregnant with their next litter.

The objectives of this study were to: (1) quantify the variation in the litter size and sex ratio of offspring; (2) examine the relationship between the number and sex ratio of litters; (3) evaluate alternative hypotheses for sex ratio variation for this population; and (4) examine the relationship between female age, weight, and condition on litter size and the sex ratio of offspring.

Methods

This study was conducted in Palo Verde National Park ($10^\circ 21'$N, $85^\circ 21'$W), Guanacaste Province, Costa Rica. For a description of the study site refer to Chapter 2.

Opossums were captured in Tomahawk live traps from 1 February to 4 August 1992, and from 20 January to 23 July 1993. Four trapping grids were established. Each grid contained 30 traps and covered a 15 ha area. All four trapping areas were sampled for 4-5 consecutive nights, six months each year, three months during the dry season (Jan-Apr) followed by three months during the wet season (May-Aug).

Opossums were processed in the field at the trap site. The processing procedures are described in Chapter 2. Physical condition of the animals was evaluated by calculating a condition index that consisted of the residuals resulting from the log of body weight $1/3$ regressed on the log of head and body length. If females carried pouch young, the offspring were counted and sexed and head-rump and tail lengths were measured to determine their weight and age (Petrides 1949, Reynolds 1945). The weight of each litter was then subtracted from the female's body weight. Parturition dates were determined by back-dating from the offspring of known age. All pouch young were toe-clipped for identification. Once the marked offspring dispersed into the adult population, they were used to verify the ages of other opossums that were aged based on molar eruption and tooth wear (Gardner 1982). Animals were processed monthly to monitor changes during the study period.

Statistical Analysis

The density of opossums in the trapping area was estimated by calculating the total number of unique individuals captured during the first three trap nights in each grid for each month. The total number of unique individuals from the four grids were pooled for

each year separately and divided by the total trapping area (60 ha). The density of opossums was compared between seasons and years using a Yate's Chi-square test. Litter sizes were compared between seasons and years using Mann Whitney U Tests. The adult sex ratios and the sex ratio of pouch young were compared with an expected 50:50 ratio using a Chi-square test. Body weight for female opossums was compared between seasons and years using a nested ANOVA (Abacus Concepts, SuperANOVA 1989). Repeated measures were averaged to obtain an independent data set. Condition was compared between seasons and years by analysis of covariance. Arsine transformations were used to normalize the sex ratios (% sons) of the litters (Sokal and Rohlf 1981). Analysis of covariance was used to evaluate the effects of litter size, maternal age, weight, and condition on the litter sex ratio. Sex ratio was the dependent variable and litter size was the covariate. Correlations were performed to determine the relationship between maternal age, weight, and condition on the litter sex ratio and litter size pooled over the entire study period (Abacus Concepts, Statview 1992).

<u>Results</u>

Litter size and the Sex Ratio of Offspring

The trapping effort and population sample sizes are described in Chapter 2. Mean litter size increased between birth periods within and between years (Table 3-1). In 1992, the mean litter size for the dry season reproductive period was 7.4 compared to 8.4 in 1993 ($Z = -1.95$, $P = .05$). For the wet season reproductive period, mean litter size in 1992 equalled 8.1 compared to 10.1 for 1993 ($Z = -2.15$, $P = .03$).

The overall sex ratio of the 1992 litters was not significantly different from 50:50 (Table 3-2). After accounting for the mortality of pouch young, a total of 132 sons and 128 daughters were produced during the dry season birth period, compared to 46 sons and

59 daughters during the wet season. Mortality of pouch young during 1992 equalled 8.1% for the dry season birth period and 6.3% for the wet period. There was no difference in the mortality between the sexes. During the 1993 dry season birth period, sons:daughters equalled 131:153, compared to 60:82 during the wet season. Mortality of pouch young was 1% and 1.4%, respectively. Although more daughters were produced by females in 1993 compared to 1992, the difference from an expected 50:50 sex ratio was not significant.

The number of biased litters was not significantly different from 50:50 (Table 3-2). Fifty-three percent of the dry season litters were male-biased in 1992 compared to 41% in 1993. For the wet season litters, exactly 50% were male-biased in 1992 compared to only 31% in 1993; however, this difference was not significant ($X^2 = 1.92, P > .10$).

Tradeoffs

There was an inverse relationship between litter size and the sex ratio (% sons) that females produced (Fig. 3-1). This inverse correlation between litter size and litter sex ratio over the entire study period was significant ($R = -.38, P < .001, N = 96$). In addition, if females produced large litters (greater than the mean litter size for a particular birth period), the mean sex ratio for these large litters was female-biased (.35 to .53; Figure 3-2). In contrast, females that had small litters (less than the mean litter size), on average produced male-biased litters (.48 to .69). These differences, however, were not significant (Fisher's Test).

Futhermore, there was a significant pattern in the sex ratios of consecutive litters produced by the same female. In general, females that produced male-biased litters during their first reproductive effort produced a smaller proportion of sons during their second reproductive effort (35% of the females vs. 5% that produced greater % sons). On the other hand, females that produced fewer than 50% sons during their first litters, produced a

greater proportion of sons in their second litters (45% of the females vs. 15% that produced fewer % sons; $P < .05$, $N = 20$).

The results of the Analysis of Covariance revealed that year and maternal weight had significant effects on litter sex ratio after accounting for their effects on litter size (Table 3-3). Litter size had the strongest effect on litter sex ratio ($F = 23.49$, $P < .001$), all other factors were not significant.

Female Condition

Females grew throughout their lifetimes and adult female body weight ranged from 0.50-2.02 kg with an average of 1.29 kg over the entire study period (Table 3-4). There was no significant difference in the weight of females between dry and wet seasons ($F = 1.97$, $P = .14$) or between years ($F = 2.62$, $P = .11$).

Females during 1992 were in better condition than females in 1993 ($F = 6.53$, $P = .01$). The mean condition index for 1992 females was .040 ($\pm$ .03, $n = 46$) compared to .022 ($\pm$ .02, $n = 53$) in 1993. If the youngest age class of females is removed, however, this difference in condition between years disappears ($F = 1.44$, $P = .23$). In 1992, females in the youngest age class comprised 19% of all the females in the population, compared to 30% for the 1993 population. The greater number of very young females during 1993 may have influenced the results. The condition of females between dry and wet seasons varied between years. The condition index increased significantly between seasons during 1992 ($F = 20.15$, $P < .001$), but not during 1993 ($F = .09$, $P = .77$). There was no significant correlation between litter size or the litter sex ratio with maternal age, weight, or condition over the entire study period (Table 3-5).

There was seasonal variation in the density of opossums in the total trapping area. There were significantly higher densities during the dry season, followed by a decrease in density during the wet season. During the dry season of 1992, density equalled 1.15

opossums trapped/hectare, decreasing to 0.87 opossums trapped/hectare during the wet season. The density in 1993 varied from 1.62 opossums trapped/hectare during the dry season to 0.67 individuals trapped/hectare during the wet season (Yates X^2 = 5.38, P < .05).

Discussion

The sex ratio of litters produced in this study was not significantly different from an expected 50:50 population-level sex ratio. Although more daughters were produced by females in 1993 than in 1992, there was no significant difference in the sex ratio of offspring (using total sons and daughters produced or number of biased litters). There was a significant inverse correlation, however, between litter size and the sex ratio produced by individual females during the study period (Figure 3-1). In general, female opossums produced large, female-biased or small, male-biased litters.

Litter Size and the Sex Ratio of Offspring

A female's fitness depends on the fitness and the number of her offspring (Smith and Fretwell 1974). If a female increases investment in individual offspring, the number she can produce decreases. Smith and Fretwell (1974) however, did not distinguish between investment in male and female offspring. If sons and daughters do not cost the same to produce, investing differentially in one sex changes both the sex ratio and number of offspring produced (Myers 1978, Clutton-Brock and Albon 1982, McGinley 1984 , Huck et al. 1990).

Virginia opossums have a polygynous mating system and males compete with each other to mate with females (Ryser 1992, Wright et al. in press). Male opossums grow faster and reach a larger adult body size compared to females (Gardner 1982, Seidensticker

et al. 1987, Ryser 1992, Wright et al. in press); and large males have greater reproductive success compared to smaller males (Ryser 1992). In this study, males were on average 28% heavier than females. Sons and daughters do not differ in size, however, during the two month pouch phase (Sunquist and Eisenberg 1993, Wright et al. in press). There is limited evidence suggesting that males begin to increase in size during the one month nest phase prior to dispersal (Ryser 1990, Sunquist and Eisenberg 1993). Therefore, although opossums are similar to other polygynous mammals in sexually dimorphic characteristics, it is not clear whether female opossums invest more in sons compared to daughters during the pre-weaning stage. If opossum sons cost more to produce than daughters, and adult females have a limited amount of energy to invest in offspring, females that produce more sons will have fewer offspring. On the other hand, females that bias their litters towards daughters will produce a greater number of offspring (Myers 1978). Consequently, females may produce either small, male-biased or large, female-biased litters.

In this study, there was an energetic tradeoff between consecutive litters and the proportion of sons produced. Females that produced male-biased litters during the first birth period of the year produced fewer sons in their second litter and vice versa. In addition, there was a significant inverse relationship between litter size & % sons (Figure 3-1). The composition of litters ranged from two (100% sons) to 14 (21% sons). Furthermore, if females produced litters that were larger than the mean litter size, these litters were, on average, female-biased, whereas small litters were male-biased (Figure 3-2). These data suggest that in this study, opossum sons were more costly to produce than daughters.

This "tradeoff" between the sex ratio (% sons) and number of offspring produced may partially account for the litter size pattern found in this study. During the first birth period of 1992, the sex ratio of offspring was 50:50 (mean litter size = 7.4) and the litters became increasingly female-biased and larger during 1993 (Tables 3-1 and 3-2). Finally,

more females, on average, produced large, female-biased litters in 1993 (56%) compared to females in 1992 (48%).

<u>Variation in the Sex Ratio</u>

Why should more females produce female-biased litters during 1993 compared to 1992? There are a variety of hypotheses addressing the facultative adjustment of sex ratios that may pertain to this population. The first two hypotheses presented here address population-level strategies and the last two address how individual females may alter the sex ratio of their offspring to maximize individual fitness. The first hypothesis deals with seasonal shifts in the sex ratio and was first formalized by Werren and Charnov (1978) and revised for opossums by Wright et al. (in press). The First Cohort Advantage hypothesis depends on a life history in which only two litters are produced during a year. Sons that are born in the first birth period of the year are older and larger than sons born during the following birth period. These size differences are maintained throughout the males' reproductive lifetime, and since size is important to a male opossum's reproductive success, first cohort males have much greater fitness (Wright et al. in press). This hypothesis predicts male-biased sex ratios for the first birth period and female-biased second litters. This hypothesis does not explain the sex ratio pattern found in my study.

Although this is a typical life history for opossums in North America, opossums in this study produced three litters in a year (Feb, May, and Aug), and first cohort males (Feb) may not have a reproductive advantage throughout their lifetimes. During the first breeding period of the year, the population of males at Palo Verde consisted of first-time breeders (males from the Feb and May cohorts of the previous year), and very old males (> 24 months) in their second reproductive year. The August cohort males include individuals that are six and 18 months old. The 18 month old males would be larger than the first-time breeders and would have a competitive advantage. Longevity in this population was 2.5

years, thus, 18 month old males do not represent senescent males, but rather, these males are likely to be serious competitors. The younger and smaller first and second cohort males are only 12 and 9 months old, respectively. Therefore, a life history containing three cohorts per year as occurs in the Palo Verde population removes or decreases the reproductive advantage predicted for males from the first cohort of the year.

The second hypothesis is the Local Resource Competition hypothesis proposed by Clark (1978) and revised by Silk (1983). This hypothesis predicts that when resources are limiting and one sex is philopatric while the other sex disperses, females should produce the sex that disperses. There has been support for this hypothesis in some primates and ungulates (Clutton-Brock and Albon 1982, Clutton-Brock and Iason 1986, Chapman et al. 1989). In the Virginia opossum, daughters are usually philopatric and sons disperse (Gardner 1982, Seidensticker et al. 1987, Wright 1989).

The Resource hypothesis considers the presence of daughters as an extension of maternal investment (Clutton-Brock and Albon 1982). It is based on the assumptions that if daughters were not produced, the unused resources would be used by the mother, and that the presence of daughters does not negatively affect the mother's future reproductive success. These assumptions are not met in this population. Virginia opossums do not defend territories (Gardner 1982, Seidensticker et al. 1987, Wright 1989, Ryser 1990). Unlike opossums in Florida, however, the home ranges of both males and females in my study overlap greatly. Opossums are opportunistic omnivores and both sexes compete with each other for the same resources. Therefore, opossum females compete for resources regularly with a few daughters and many unrelated individuals. Although the adult population was significantly male-biased during 1993, this does not imply that there were additional resources for females.

A third hypothesis involves maternal condition. According to Trivers and Willard (1973), in polygynous mammals large males have much greater potential reproductive success compared to females. If a female can produce large, competitive sons, her fitness

will be much greater than if she produced large daughters because size is not an important factor in a female's reproductive success. This hypothesis assumes that sons are more expensive to produce, that above average mothers (in weight or condition) can produce large sons, and that the differences in parental investment will be maintained in the offspring throughout adulthood.

There has been support for this hypothesis in a variety of mammals (Rivers and Crawford 1974, McClure 1981, Labov et al. 1986, Austad and Sunquist 1986, Wiley and Clapham 1993). But a large number of studies fail to support Trivers and Willard (Clutton-Brock and Iason 1986). Studies of opossums in Florida failed to find support for a female condition hypothesis (Sunquist and Eisenberg 1993, Wright et al. in press). This study failed to find any correlations with sex ratio and female weight, condition, or age. There was no evidence that suggests that female condition as measured by body size or weight may be a factor influencing the sex ratios produced.

The final hypothesis that may pertain to this population is a Disturbance hypothesis proposed by Werren and Charnov (1978). They describe a situation where a natural perturbation affects the sexes differentially and one sex suffers greater mortality. This would create a bias in the adult population and females would maximize their fitness if they could perceive the change in the adult sex ratio and produce the scarce sex. In this study, the adult population sex ratio and structure differed significantly between years. In 1992, the adult sex ratio did not differ significantly from 50:50. In 1993, however, the adult sex ratio was significantly male-biased (92m:54f, $P < .01$).

In a population where there are significantly fewer adult females, as in 1993, there should be selection for females to respond by producing more daughters. Females producing daughters would have higher fitness relative to others in the population. This hypothesis assumes that individuals would be able to recognize the current population sex ratio. In this study, the home ranges of males and females overlapped extensively. Males were much larger than females at all adult age classes and possess sternal scent glands

(Holmes 1992). Individuals could encounter each other as they forage or look for den sites (opossums change dens regularly; Hossler et al. 1993), or encounter individual scents. In Palo Verde, where individuals converge on the water holes during the dry season, the frequency of encounter rates is very high. Therefore, the sexually dimorphic characters, social structure, and habits of this species provide a mechanism whereby individuals can assess the relative proportion of males and females in the population within a given year. The production of female-biased litters in 1993 may, in part, be due to the absence of females in the adult population and a response by many of the remaining females to produce the scarce sex.

In summary, factors such as female condition, weight, or age do not seem to be important factors affecting the sex ratio of offspring in the Virginia opossum (Sunquist and Eisenberg 1993, Wright et al. in press, this study). Particular life histories may favor seasonal shifts in the sex ratio (Wright et al. in press), however, the population at Palo Verde had a life history that differed from that reported for opossums in North America and did not support a seasonal shift hypothesis. An inequality in the adult sex ratio has not been evaluated as an alternative hypothesis for sex ratio variation in wild opossums. Typically, the adult population sex ratio is not significantly different from 50:50. During 1993, however, the opossums in this study supported the conditions and predictions expected under a Disturbance Hypothesis proposed by Werren and Charnov (1978). There were significantly more adult males in the population and females, on average, produced female-biased litters.

To maximize reproductive success, there should be selection on females to alter the sex ratio of their offspring to capitalize on current ecological circumstances. In this study, females produced 50:50 offspring sex ratios during 1992 and produced more female-biased litters during 1993. Since the data suggest that sons cost more to produce than daughters, the larger litter sizes produced during 1993 may, in part, be due to the greater production of daughters that year. There are additional factors, however, that may influence litter size.

The significant increases in mean litter size between and within years in this study may reflect differences in maternal weight, age or condition.

Litter Size Variation

The seasonal variation in litter size found in this study (small, dry season litters vs. large, wet season litters), is unusual for Virginia opossums. Opossums in Florida produce consistent litter sizes throughout the year (mean = 6.75 and 6.56 for first and second litters, respectively; Sunquist and Eisenberg 1993, Wright et al. in press). Maternal weight or condition are important factors that may affect litter size. In small mammals, females in poor condition, and food-restricted females produce and wean fewer young than those in good condition (Rivers and Crawford 1974, McClure 1981, Labov et al. 1986). Seasonal variation in litter size is common among meadow voles (Microtus pennsylvanicus), and maternal and neonatal mass explained one half of this litter size variation (Dobson and Myers 1989). In the didelphid marsupial Caluromys philander, the food intake of females was positively correlated with litter mass, and the offspring of small litters were larger than the offspring of large litters (Atramentowicz 1992).

Tropical dry forests are characterized by pronounced seasonality in rainfall (Janzen 1983). Palo Verde usually receives less than 2 m of rainfall during the wet season and no rainfall during the six month dry season (Janzen 1983, Gill 1988). This results in seasonal differences in the availability of resources. Insect densities are at their highest during the beginning of the wet season and decline during the rest of the year (Janzen 1983). The pattern of fruit availability is similar but more variable. For mammals, the dry season is an especially stressful period in tropical dry forests (Janzen 1983).

In this study, the first litter of the year occurred during the last three months (Feb-Apr) of the dry season. During this time, the only water in the study area was restricted to water holes (pers obs.). The opossums had to travel to these specific areas for water on a

regular basis. As a result, the animals became very concentrated around the water holes during the dry season, and their density in this area increased. Once the rains began in May (the beginning of the second birth period), water was widely distributed, the animals dispersed, and density decreased. Therefore, if resources such as water are limited during the dry season, and animals become more concentrated, this could increase competition and aggressive interactions among individuals that could, in turn, result in decreases in body weight and/or condition. Since large litters are energetically expensive to produce, seasonal variance in litter size may reflect seasonal differences in maternal weight or condition that may be a result of seasonal differences in resources.

Overall, female body weight did not change significantly between dry and wet season birth periods. In general, female opossums grew throughout their first reproductive year. Only 17% of the female population survived to a second reproductive year. In contrast, these older females ($\geq$ 24 months) lost weight (and died) during the study period.

The condition indices varied inconsistently between seasons, increasing from dry to wet season in 1992 but not during 1993. Condition based on body size measurements (weight and head and body length) may not be true measures of a female opossum's physical condition. Furthermore, condition and body size, in general, were not correlated with female reproductive success in other studies of Virginia opossums (Sunquist and Eisenberg 1993, Wright et al. in press). Female condition based on a measurement of hind leg fat was positively correlated with litter size in a study of the Virginia opossum in New York (Hossler et al. 1994). It may be more difficult, however, to assess condition using this method in tropical populations where considerably less fat is laid down compared to opossums in temperate areas (Janzen 1983).

Litter size may also be correlated with maternal age (Snyder 1962, Sherman and Morton 1984, Armitage 1987, Dobson and Myers 1989). There was a trend for the oldest females to produce larger litters, but this was only significant for one reproductive period out of four (wet season 1992). Overall, litter size was not significantly correlated with

maternal age in this study (R = -.021, P = .8396; Table 3-5). In contrast, there was a trend for older female opossums in Florida to produce smaller litters (Wright et al. in press). In the present study, there was considerable variation in female weight, condition, and age, and in the number of offspring produced. Litter size, however, was not significantly correlated with a female's weight, condition, or her age.

The increase in litter size from the dry to the wet season may involve more than a response to available resources. The increase in litter size could be the result of selection on females to produce larger litters during a time when survival of offspring is maximized. During the wet season reproductive period, females produced from two to 14 offspring. If females are only responding to current resources, those that conceive during the last weeks of April (the end of the dry season) should have smaller litters compared to females that conceived during the first weeks in May (the beginning of the wet season).

During 1992, breeding was very synchronous and all females conceived in May. In 1993, however, one third of the females conceived during the last two weeks of the dry season (April), and their litter sizes were not significantly different from those of females that conceived in May (mean = 9.6 vs. 10.4, respectively). In fact, the litter sizes produced by females that conceived during the end of the dry season were weighted by one female that had a litter size of three while all others ranged from 10 to 12. Therefore, in an environment with profound yet predictable seasonal differences in rainfall and resources, there may be selection for all females regardless of size, condition, or age to produce larger litters during the wet season when resources are plentiful, compared to the dry season where resources, cover, and especially water are scarce.

In addition to seasonal variation in litter size, overall litter sizes were greater during 1993 compared to 1992 (Table 3-1). This may be due to differences in resources between years. If 1993 was a "better" year this was not translated into differences in female weight or condition. There was a highly significant (P < .001) inverse correlation between litter size and litter sex ratio in this study. A multiple analysis of covariance revealed that

maternal weight and year were also significant factors affecting this relationship. Maternal weight, however, did not differ significantly during this study and even if significant differences in female weight or condition had been apparent between years, these factors were not correlated with litter size in this study. The seasonal and yearly differences in mean litter size in the present study cannot be explained by differences in maternal weight, age, or condition. The differential cost of producing sons and daughters and the tradeoff between offspring sex ratio and litter size is consistent with the litter size pattern observed in this study, suggesting that sex ratio of offspring may be an important factor affecting litter size (Myers 1978, McGinley 1984, Armitage 1987, Huck et al. 1990).

To date, the studies of the reproductive strategies of female opossums have examined facultative sex ratio variation (Austad and Sunquist 1986, Sunquist and Eisenberg 1993, Wright et al. in press). In nature, it is likely that several factors affect a female's reproductive decisions. In addition to the sex ratio of offspring, the litter size is also an important factor affecting a female's fitness. If sons and daughters do not cost the same to produce, investing differentially in one sex will alter both the sex ratio and the number of offspring produced. This study provides an example, as proposed by Zhang and Wang (1994), of the need to consider the relationship between life-history evolutionary theory and sex allocation theory when examining the reproductive decisions of sexually producing organisms.

Table 3-1. Summary of litter sizes produced by opossums (<u>Didelphis</u> <u>virginiana</u>) during dry and wet season birth periods, 1992-1993, Palo Verde National Park, Costa Rica.

	Mean Litter Size	SD	Mode	Range	N
1992					
Dry	7.4	1.95	9	3-11	35
Wet	8.1	2.72	10	2-11	13
1993					
Dry	8.4	0.98	8	6-10	34
Wet	10.1	2.74	10	3-14	14

Mann Whitney U Tests:
[a]Dry season litter sizes between years: $Z = -1.95$, $P = .05$.
[b]Wet season litter sizes between years: $Z = -2.15$, $P = .03$.

Table 3-2. Summary of the sex ratios of offspring produced by opossums (Didelphis virginiana) during dry and wet season birth periods, 1992-1993, Palo Verde National Park, Costa Rica.

	Total M:F	N	Chi-Square	P	Male-biased Litters
1992					
Dry	132:128	35	0.62	ns	53%
Wet	46:59	13	1.61	ns	50%
1993					
Dry	131:153	34	1.70	ns	41%
Wet	60:82	14	3.40	ns	31%
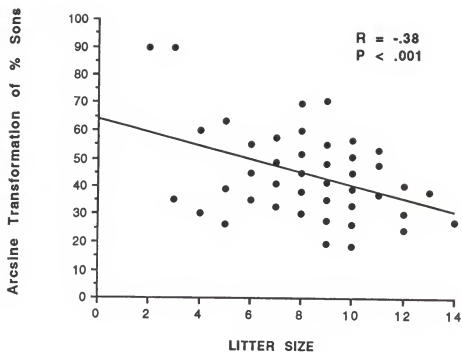
Figure 3-1. Inverse correltation between litter size and the sex ratio (arcsine transformation of % sons) for all litters (n=96) during the first two birth periods of 1992 and 1993.
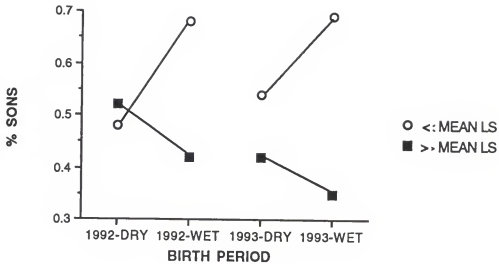
Figure 3-2. Mean percent sons (sex ratio) for two groups of female Virginia opossums: 1) females that had smaller litter sizes than the mean, represented by the open circles; and 2) females that had greater than the mean litter sizes, represented by the solid squares, for the first two birth periods of 1992 and 1993.

Table 3-3. ANCOVA results of the effects of year, season, maternal age, weight, and condition on litter size and the sex ratio in Virginia opossums during 1992 and 1993. Litter sex ratio is the dependent variable and litter size is the covariable.

Effect	df	F-Value	P-Value
Year	1	4.893	.0296
Season	1	1.079	.3018
Maternal Age	1	.972	.3268
Weight	1	6.251	.0143
Condition	1	.435	.5115
Litter Size	1	23.489	.0001
N	96		

Table 3-4. Mean weights (kgs) of female opossums (Didelphis virginiana) during the dry and wet season at Palo Verde National Park, Costa Rica, 1992 and 1993.

Female Age Class[a]	1992						1993					
	Dry			Wet			Dry			Wet		
	WT	SD	N	WT	SD	N	WT	SD	N	WT	SD	N
1	0.84	.13	7	1.29	.11	5	0.91	.24	9	1.05	.30	12
2	1.20	.12	10	1.31	.14	12	1.20	.27	23	1.48	.17	14
3	1.42	.17	14	1.55	.27	10	1.36	.24	3	1.52	.03	3
4	1.69	.20	7	1.59	.22	5	1.70	.17	8	1.54	.13	3
ALL	1.31	.32	38	1.43	.23	32	1.24	.35	43	1.33	.30	32

[a] Age class 1 = 6 months, 2 = 9 month, 3 = 12 months, 4 = 24 months, at beginning of the study period.

Table 3-5. Correlations between litter size and the sex ratio of offspring with female age, weight, and condition during the first two birth periods of 1992 and 1993 combined, N = 96.

Litter Size and Female:	R	F-Value	P-Value
Age	-.021	.041	.8396
Weight	.070	.468	.4957
Condition	-.136	1.768	.1868
Sex Ratio and Female:			
Age	.092	.810	.3704
Weight	.180	3.140	.0795
Condition	.099	.937	.3356

VARIATION IN SEXUALLY DIMORPHIC CHARACTERS AMONG MALE VIRGINIA OPOSSUMS

Introduction

Opossums have several sexually dimorphic characters that show considerable individual variation. There is little information on the extent of variation among males in sexually dimorphic characters in the Virginia opossum (Didelphis virginiana). This variation may indicate differences in relative reproductive success among individuals.

Sexually dimorphic characters have typically been attributed to sexual selection (Darwin 1871, Mayr 1972, Trivers 1972). According to sexual selection theory, when there is a great asymmetry between the sexes in the amount of parental investment given to their offspring, the sex that invests less will have greater reproductive success by maximizing numbers of matings (Trivers 1972). In mammals, males generally do not invest further in their offspring after copulation. Darwin (1871) predicted that in such cases, males should compete with each other to mate with females. Under these conditions, there should be selection for large body size, ornaments, and weapons (horns, teeth) in males and, in general, a polygynous mating system (Darwin 1871, Mayr 1972, Trivers 1972). In a review of sexual dimorphism in mammals, Ralls (1977) found that, contrary to Trivers' hypothesis (1972), parental investment was a poor predictor of polygyny and sexual dimorphism. Despite these criticisms, opossums seem to support the conditions and predictions of sexual selection theory (Mayr 1972, Trivers 1972).

The Virginia opossum is a nocturnal, solitary, species with a polygynous mating system (McManus 1974, Gardner 1982, Seidensticker et al. 1987). Several males gather around a female in estrus and fight with each other, and the largest male generally wins and

mates with the female (Ryser 1992). After fertilization, there is no further investment in offspring by males (Gardner 1982, Austad and Sunquist 1986, Seidensticker et al. 1987, Ryser 1992).

Reproductive success in opossums varies more in males than in females. Larger males have greater reproductive success (Ryser 1992), whereas body size is not an important factor affecting a female's reproductive success (Gardner 1982, Seidensticker et al. 1987, Sunquist and Eisenberg 1993, Wright et al. in press). Therefore, there should be selection for large body size in males and not in females. In Virginia opossums, males are significantly larger than females (Gardner 1973, Gardner 1982, Seidensticker et al. 1987, Ryser 1992). In addition to body size, male opossums have significantly larger canine teeth compared to females.

It is not always clear, however, how additional dimorphic characters are related to sexual dimorphism in body size (Ralls 1977). Canine teeth are often sexually dimorphic but this difference may be due to differences in body size alone. Canines are used for feeding, in threat displays, and in actual fights by many mammals including opossums (Ralls 1977, Van Valkenburgh and Ruff 1987, Shine 1989, Ryser 1990, Dinerstein 1991). Differences in feeding habits, however, may lead to dimorphism in canines, but the direction of the size difference between the sexes is difficult to predict, and the ecological causation model is difficult to test (Shine 1989). Many studies of opossums have noted that males' canines are significantly larger than those of females (Gardner 1982, Ryser 1990), but there has been no attempt to determine how the sexual dimorphism in canine size is related to body size differences.

In addition to variation in body and canine size, males may differ in the size of their sternal stain. Male opossums possess sternal glands that exude a musky odor and create a visible stain over the chest of individuals (Holmes 1992). The sternal glands are found exclusively in males and the stained area may vary in appearance, and perhaps odor, among individuals and throughout the year (Holmes Meisner 1986). There has been no attempt,

however, to quantify the size of the sternal stain among individual males of different age classes, nor to follow the changes within a population in the wild.

Sexually dimorphic characters such as body size, canine length, and sternal stain appearance may all convey information about the sex, condition, and dominance status of the individual (Ralls 1971, Hebert and Barette 1989, Bartecki and Heymann 1990, Rozenfeld and Rasmont 1991, Herrera 1992, Holmes 1992). By examining differences between the sexes it may be possible to determine whether these differences are due directly to sexual selection, or whether they are merely correlated with differences in overall body size, or both. Furthermore, comparing differences in these characters among males within a population may help to explain the role these structures play in the reproductive success of individuals.

To examine the dimorphic characters between sexes and among individual males I (1) compared the weight, head and body length, and canine length between the sexes and among males of different age classes; (2) determined whether canine length is larger in males than expected due to differences in body size alone; (3) described the ontogeny of the sternal stain in a population of male opossums; and (4) quantified the variation in sternal stain size both within males of different age classes and during the breeding and nonbreeding seasons.

Methods

This study was conducted in Palo Verde National Park (10°21'N, 85°21'W), Guanacaste Province, Costa Rica. For a description of the study area refer to Chapter 2.

Opossums were captured in Tomahawk live traps from 1 February to 4 August 1992, and from 20 January to 23 July 1993. Four, 15 ha grids were established each containing 30 traps. Traps were set for 4-5 consecutive nights in a grid, then rotated to the next grid for an equal amount of time. All four trapping areas were sampled in this manner

for six months each year, three months during the dry season (Jan-Apr) followed by three months during the wet season (May-Aug).

Opossums were processed in the field. Processing procedures are described in Chapter 2. Head and body length was measured from the tip of the nose to the base of the tail along the dorsal side (straightening the animal's back as much as possible). Length of the canine was measured from the gum line to the tip of the tooth.

The sternal stain was measured in all males by placing a transparent piece of plastic over the area and tracing the outline of the stained area with a permanent marker. The traced stain was then transferred onto paper and the area was computed in cm^2 using a computer program. The color of the stain was compared to a standard paint color chart and the matching color was recorded. This procedure was repeated monthly on all captured males to follow changes in sternal stain during breeding and nonbreeding seasons.

Statistical Analysis

Weight, head and body length, and canine length were compared between the sexes and among males of different age classes with analysis of variance (Abacus Concepts, SuperANOVA 1989). Growth was compared between the sexes by plotting the mean log of weight of males and females by month; the relationships were then compared by analysis of covariance.

The relationship between canine length and body length was examined by regressing the log of canine length on log of head and body length. The regression equations generated for males and females were compared by analysis of covariance. If the observed slopes were significantly different from a slope of one, the relationship was considered allometric. The size of the sternal stain was compared among males of different age classes with the Kruskal-Wallis test. The relationship between the size of the sternal stain and body size was examined among males by regressing log of the sternal stain area

on log of head and body length. Ninety percent confidence intervals were calculated to determine whether the relationship was isometric or allometric. If the observed slope was significantly different from a slope of two, the relationship between log sternal stain area and log of head and body length was considered to be allometric.

Results

There was a significant size dimorphism between the sexes (Table 4-1). Males had greater head and body lengths and weighed 28% more, on average, than females (1992: $F_{wt} = 50.57$, $F_{hb} = 15.98$; 1993: $F_{wt} = 31.04$, $F_{hb} = 16.60$, P < .001). During the study period males ranged from a mean body weight of 1.14 to 2.38 kg. Males of different age classes differed significantly in weight and in head and body length (P < .001; Table 4-1) during both 1992 and 1993. Maximum body weights during the study period equalled 3.0 kg for males and 2.2 kg for females.

In general, males and females increased in body size during the study period (Figs. 4-1a and b). Weight per month differed significantly between the sexes in both years (F = 31.72, P < .001, 1992 and F = 15.55, P = .004, 1993) The difference, however, was in the y-intercepts, and there was no significant difference in the slopes (i.e. growth rates) of males and females (P = .75, 1992 and P = .65, 1993). In contrast, males in the youngest two age classes grew throughout the study period. Males in the oldest age classes were larger than younger males in February, but, instead of increasing they maintained their weight throughout the study period (Figs. 4-2a and b).

Males had significantly larger canine teeth compared to females. During 1992, mean canine length measured 14 mm ($\pm$ 2.5) for males compared to a mean of 9 mm ($\pm$ 2.5) for females (F = 120.70, P < .001). Mean canine length was similar during 1993, 13 mm ($\pm$ .3.7) versus 8 mm ($\pm$ .1.6) for males and females, respectively (F = 16.60, P <

.001). Maximum canine lengths during the study period were 21 mm for males and 18 mm for females.

There was a significant relationship between log of canine length and log of head and body length for males and females during 1992 and 1993 (P < .001; Figs. 4-3a and b, respectively). There was an allometric relationship between log canine length and long head and body length for males during both years. During 1992, the 90% confidence interval for the male slope was 1.48 to 2.29 and for 1993, the 90% confidence interval was 2.00 to 2.45. The female slopes did not differ significantly from a slope of one (1992, 90% CI = .85-1.45; 1993, .94-1.69). During 1993, there was a significant interaction between sex and head and body length on canine length (F $_{slope}$ = 12.73, P < .001).

Sternal stains first appeared in males when they were five months old and increased in size until males were two years old, then began to decline in size or disappear (Table 4-2). In three of the nine oldest males (> 2 years of age), there was no apparent sternal stain early in the breeding season but it appeared about two weeks later. In contrast, all younger males always had a sternal stain. In general, sternal stains increased isometrically with an increase in head and body length (F = 34.34, P < .001, n = 80; Fig. 4-4). There was no significant difference, however, in the size of the sternal stain among males according to age class (H = 6.67, P = .08, Fig. 4-5).

Discussion

Variation in Body Size

The sexual dimorphism in body size found in this study is consistent with what is known for the Virginia opossum (Gardner 1982; Seidensticker et al. 1987). In general, it is stated that opossums grow throughout their life time (ca. 2.5 years in this study).

Indeed, on average, all males and females increased in weight during this study, and males were consistently larger than females.

Because male and female opossums do not differ in size during the pouch phase, and differences are slight at weaning (Ryser 1990, Sunquist and Eisenberg 1993, Wright et al. in press), the apparent size dimorphism in adults must be acquired through fast male growth rates during the postweaning period. The growth rates in this study, however, were not different for males and females (Figs. 4-1a and b). This study covered the first two reproductive periods for this population, and adults ranged in age from six to 28 months during this time. Therefore, males must grow significantly faster than females from the moment they disperse (100 days old) until they reach six months of age, a period of only three months. In Florida, Ryser (1990) found that males of all age classes had faster growth rates than females from 150 to 250 days of age.

The apparent increase in body size throughout life was not consistent among age classes (Figs. 4-2a and b). Data on the variation in body size among individuals of different age classes within a population are generally lacking for the Virginia opossum. Studies in Florida indicate that there are significant differences in body size among individuals from different cohorts (Ryser 1990, Sunquist and Eisenberg 1993), and these differences persist throughout the animals' life (Wright et al. in press).

In general, Virginia opossums in North America consist of three adult age classes (Gardner 1982, Seidensticker et al. 1987, Ryser (1990), Sunquist and Eisenberg 1993, Wright et al. in press). There are two birth cohorts during a year and a minority of adults survive into a second reproductive year. In this study, however, the population contained an additional cohort that resulted from a third reproductive period during the year. In February, the beginning of the first reproductive period, adults consisted of individuals who were six, nine, 12, and 24 months of age (age classes 1-4, respectively). Age classes 1 and 2 grew throughout the study period, whereas classes 3 and 4 maintained their weight (Figs. 4-2a and b). Ryser (1990) found that younger males (age class 2 in this study) had

faster growth rates than older males. He also found that only the older males (age class 3) lost weight during the breeding season, indicating that they were actively engaged in mating activities.

The mating behavior of male Virginia opossums has been studied in Florida by Ryser (1990, 1992). According to him, male opossums increased their home ranges during the breeding season to incorporate the home ranges of five to seven females. They wandered extensively during this time looking for females in estrous. The sizes of the home ranges did not differ among males of different age classes. When a female came into estrus, several males approached her, and aggressive interactions began, terminating with a successful mating by the largest male in the group. Dominant males averaged 3.18 kg compared to 2.65 kg for unsuccessful males.

Males at Palo Verde had similar body size and growth patterns during and after the breeding seasons. In this study, the oldest males (age classes 3 and 4) weighed on average 14-52% more than the youngest males. Older males did not increase in weight during or after the first two breeding seasons of the year. Only the youngest males (age class 1 and 2) grew throughout the study period, and did not show seasonal declines corresponding with the mating periods. This may indicate that the oldest, largest males are more actively involved in mating than the younger males.

Sexual Dimorphism in Canine Length

The sexual dimorphism in body size found in the Virginia opossum has usually been attributed to sexual selection (Ryser 1992). Opossums are solitary and after fertilization males do not invest further in their offspring. Males are limited by the number of estrous females that occur in their home range and by their ability to monitor this area. During the mating period several males fight with each other to mate with estrous females and reproductive success varies greatly among individual males (Ryser 1992). Larger

males enjoy greater reproductive success; therefore, there should be selection for larger body size in males.

The size of the canines could differ significantly between the sexes due simply to differences in body size, but this was not the case in this study. Canines are used in agonistic encounters in this species in the form of threat displays and in actual fights (Gardner 1982). Because of their importance in advertisement and fighting, male canines may be even larger than expected based on body size differences alone. In this study, the data support this prediction (Figs. 4-3a and b). In both years, the relationship between canine length and head and body length for males was allometric. In contrast, the canine lengths of females increased in size isometrically with body size. This suggests that there has been selection for large canine size in males as a secondary sexual characteristic. Males with larger canines may win more aggressive encounters with conspecifics and enjoy greater reproductive success.

Sexually dimorphic structures, however, may also be due to ecological differences between the sexes (Selander 1966, Shine 1989), but the ecological causation theory has been criticized because it lacks parsimony and is difficult to test (Shine 1989). Since canine teeth are used in feeding, the differences observed between the sexes may be due to differences in foraging behavior and diet. Opossums are generalists in their feeding habits (McManus 1974, Gardner 1982, Seidensticker et al. 1987), and are considered opportunistic omnivores and terrestrial "gleaners". Many studies of the diets of opossums have failed to reveal any sexual differences in feeding or intraspecific niche partitioning that could account for the large difference in canine size (Garder 1982, Seidensticker et al. 1987).

Variation in the Sternal Stain

Only male Virginia opossums possess a sternal gland that exudes a musky odor and stains the chest a yellow/orange color (Holmes Meisner 1986, Holmes 1992). Although mammalian glands are generally correlated with sexual maturity and testosterone levels (Herrera 1992), this gland appears to be active several months before males reach sexual maturity in this species. In this study, the sternal stain first appeared in males when they were five months old, but males do not become sexually mature until they are eight months old (Gardner 1982, Seidensticker et al. 1987). Holmes Meisner (1986) observed five-month-old male opossums scent marking objects in captivity with the sternal gland.

Although mammals have well developed olfactory senses and chemical communication is considered important, the specific functions of many scent glands are still poorly understood (Ralls 1971, Brown 1979, Muller-Schwarze 1983). Didelphid marsupials contain sternal glands, anal sacs, foot-pad glands, and proctodeal glands (Muller-Schwarze 1983). Opossums may use these glands to mark home ranges that may aid in the spacing of animals, or in orientation by following odor gradients (Ralls 1971, Brown 1979, Muller-Schwarze 1983, Benhamou 1989, de Monte and Roeder 1993). Furthermore, the information contained in a scent may convey the sex, condition, or social status of an individual (Ralls 1971, Hebert and Barette 1989, Bartecki and Heymann 1990, Rozenfeld and Rasmont 1991, Herrera 1992, Holmes 1992).

Many studies have shown that dominant individuals scent mark more frequently than subordinants. This may help a female recognize a male's scent, and females may reduce aggressive behaviors toward familiar males during mating (Brown 1979, Muller-Schwarze 1983, Fadem and Cole 1985, Lode 1991, Tang-Martinez et al. 1993). Sternal gland secretion, sternal stain size, and scent marking rates peaked prior to the first reproductive period, then declined (Holmes Meisner 1986, Holmes 1992).

In contrast, during this study the sternal stain was smallest prior to the first reproductive season and increased in size during the year in males of all age classes. The size of the sternal stain was significantly correlated with body size, which increased isometrically during this time. There was considerable variation among individuals, but a few trends were apparent. In general, the sternal stain increased steadily in size throughout both reproductive periods in the youngest males (age classes 1 and 2). In contrast the oldest males (age class 4) began the first mating season with sternal stains smaller than the prime age males, the sternal size then increased rapidly and declined prior to the animals' death. In contrast, the sternal stains of the two prime age classes of males (3 and 4) varied seasonally with peaks during the mating seasons, but the patterns were not striking (Fig. 4-5).

Holmes (1992) found that female opossums could distinguish between the sternal scents of males and females. A histological examination revealed that the cutaneous glands of the sternal area were much less developed in females than in males (Holmes Meisner 1986), indicating that female opossums may be able to distinguish the sex of individuals based on scent alone. In addition, there was large variation in the numbers and types of sternal gland units among males, and this may be a source of variation among individual male scents (Holmes Meisner 1986). In this study, the size of the sternal stains varied within and between age classes. The stain appeared early in a male's life, varied seasonally in prime age adults, and senesced as individuals reached the last months of life. This suggests that the sternal stain may be important in advertisement of the sex, condition, and perhaps dominance status of individual males.

Virginia opossums are sexually dimorphic. Male opossums in this study were significantly larger and had larger canine teeth than females. Males alone possess sternal glands that exude a musky odor and stain the individual's chest. The evidence suggests that these sexually dimorphic traits may be products of sexual selection, and males with larger body and canine sizes may be more successful in competing with other males to

acquire mates. These dimorphic characters not only differed significantly between the sexes, but also varied significantly among males. There were four age classes in the population of opossums in Palo Verde and the males differed significantly in size among these age classes. Very young males grew continually during the study period, whereas older males reached a maximum size and did not increase during or after the breeding seasons. Finally, males varied in the appearance and size of their sternal stains. Together with body and canine size, the sternal stain may advertise the dominance, condition, or age of males to conspecifics.

Table 4-1. A comparison of body size among males of different age classes, and between the sexes in the Virginia opossum (<u>Didelphis virginiana</u>), Palo Verde National Park, Costa Rica, 1992-1993.

Age Class	Mean WT (kg)	SD	Mean HB Length (mm)	SD	n
1992					
1	1.15	.25	326	47	8
2	1.76	.25	393	21	20
3	2.04	.24	417	22	26
4	2.38	.25	440	19	9
All Males[a]	1.89	.42	401	41	63
All Females	1.37	.30	371	35	47
1993					
1	1.14	.37	345	38	30
2	1.62	.33	389	21	21
3	2.08	.33	424	23	23
4	2.29	.31	438	20	17
All Males[b]	1.70	.57	393	47	91
All Females	1.23	.35	359	40	53

[a] $F_{WT} = 40.74$, $F_{HB} = 27.68$, $P < .001$

[b] $F_{WT} = 54.10$, $F_{HB} = 53.47$, $P < .001$
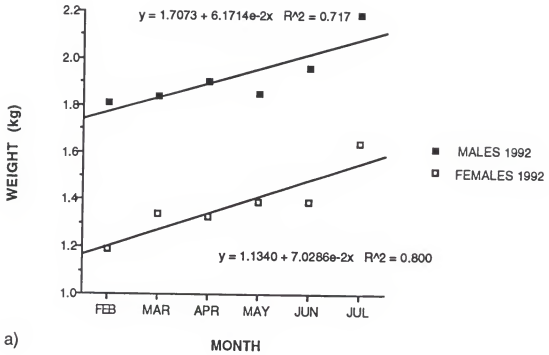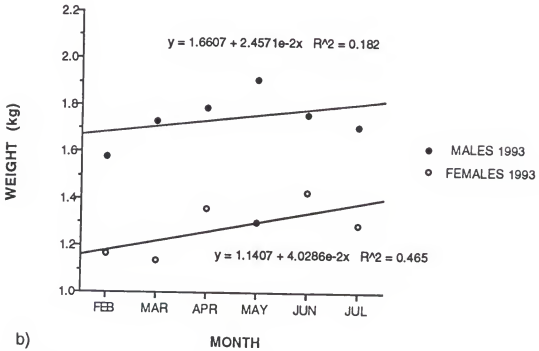
Figure 4-1. Mean weights of male and female Virginia opossums from February to July, (a) 1992 and (b) 1993, Palo Verde National Park, Costa Rica.
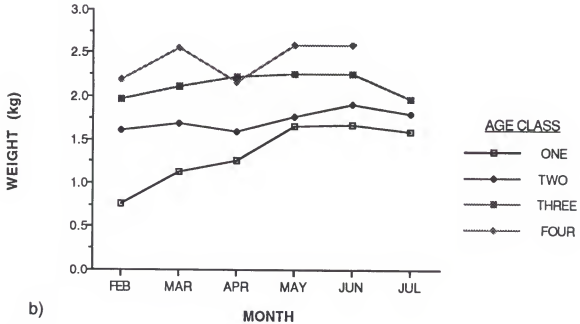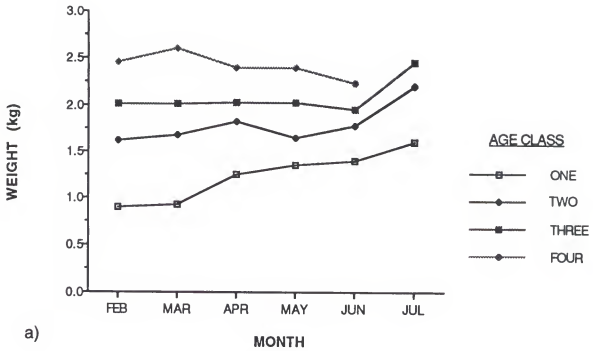
Figure 4-2. Monthly mean weights of male Virginia opossums according to age class (1 = youngest to 4 = oldest age class), during (a) 1992 and (b) 1993.
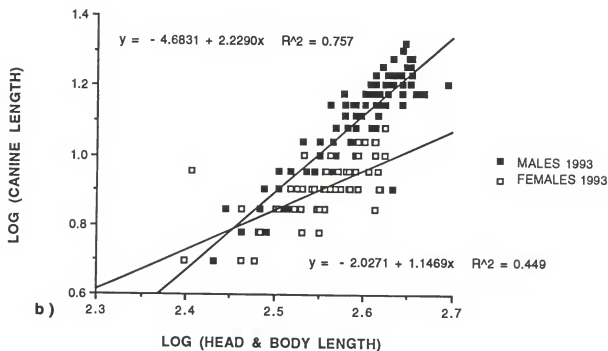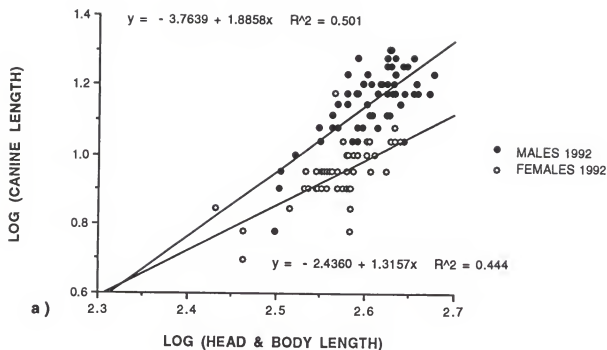
Figure 4-3. The relationship between log of canine length and log of head and body length for male and female Virginia opossums during (a) 1992 and (b) 1993.

Table. 4-2. Mean sternal-stain areas (cm^2) of male Virginia opossums (Didelphis virginiana) according to age class from January to June, 1993.

Age Class	January		February		March	
	Mean	SD	Mean	SD	Mean	SD
1	4.16	2.17	7.08	3.15	11.41	5.38
2	11.81	3.33	12.92	3.59	9.75	3.09
3	14.32	6.89	15.47	4.36	15.72	2.39
4	10.26	9.92	16.24	11.79	26.26	8.70
All Males	10.82	7.25	12.54	7.35	15.16	7.97

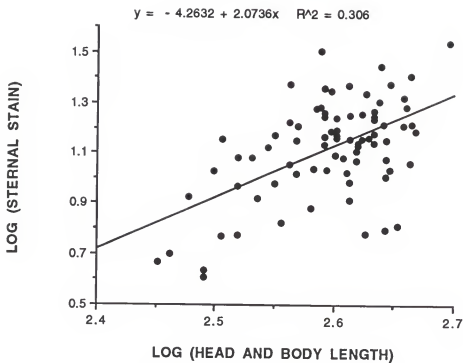| Age Class	April		May		June	
	Mean	SD	Mean	SD	Mean	SD
1	14.25	4.55	17.57	6.00	16.24	1.93
2	17.06	11.49	20.81	15.21	15.41	3.71
3	17.53	3.53	20.05	3.24	14.53	2.83
4	17.18	2.66	11.07	5.95	-	-
All Males	16.18	5.64	18.19	8.57	-	-

Figure 4-4. The relationship between log of sternal stain area and log of head and body length for male Virginia opossums during 1993.
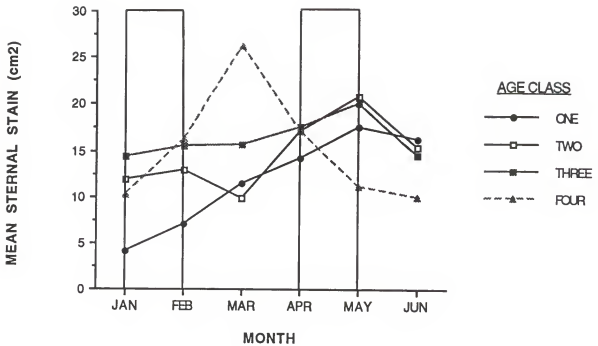
Figure 4-5. Change in the size of the sternal stain area among male Virginia opossums of different age classes during the breeding and nonbreeding season, Palo Verde National Park, Costa Rica, 1993. Breeding season from Jan-Feb and Apr-May.

The Virginia opossum has a wide distribution extending from the temperate, northern climates of southern Canada to the tropics of Costa Rica. Many aspects of the life history of this species including morphology and reproduction vary latitudinally. Much of the information concerning the Virginia opossum comes from studies of populations in North America. Selection pressures should differ, however, across this species' range and many of the life history characters may differ at the southern limits of the Virginia opossum's distribution.

This study examined the morphology, female reproductive strategies, and male dimorphic characters of Virginia opossums in Costa Rica. I used live traps and mark-recapture methods to study a population of opossums in a tropical dry forest. Tropical dry forests are characterized by extended five to six month dry seasons. The dry season at Palo Verde National Park occurs from November to April, followed by a six month wet season during which time there is less than two meters of rainfall annually.

The first objective of this study was to describe the morphology and reproductive pattern of the Virginia opossum in Palo Verde National Park. Males were significantly larger than females across all age classes. The morphological variation found in this study was consistent with what is known for the Virginia opossum. The relative sizes of opossums in Palo Verde followed a general latitudinal trend in this species of decreasing body size and increasing tail length from north to south.

Females reproduced when they reached sexual maturity at six months of age. Opossums lived for 2 to 2.5 years and females can typically produce three or four litters during their lifetimes. This contrasts with a maximum production of two litters in a

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female's lifetime in North American populations. The additional period of reproduction results in an additional age class present in the adult population. In general, a female opossum's opportunity to reproduce increases from north to south along the species' range. Since at least 100 days are required from conception to weaning, females can produce a maximum of three litters during a calendar year. In Palo Verde, females seem to reach the maximum reproductive potential reported for this species by producing three, large litters per year.

The second objective of this study was to examine the reproductive strategies of female opossums. To maximize fitness, there should be selection on females to produce the maximum number of offspring in their lifetimes. Under particular ecological circumstances, however, females may increase their fitness by producing more sons or daughters. If sons and daughters require different amounts of investment, there will be a tradeoff between the sex ratio and number of offspring produced. In this study, there was an inverse relationship between the number of offspring and the % sons produced.

Unlike populations in North America, there was seasonal variation in litter size in this study. On average, all females produced small, dry season litters and large, wet season litters. Litter size was not correlated with a female's weight, condition, or age. This tradeoff between the sex ratio (% sons) and number of offspring produced may partially account for the litter size pattern found in this study. During the first birth period of 1992, the sex ratio of offspring was 50:50 and mean litter size was 7.4. The litters became increasingly female-biased and larger during 1993. Finally, more females on average, produced large, female-biased litters in 1993 (56%) compared to females in 1992 (48%).

To examine why more females should produce female-biased litters during 1993 compared to 1992, alternative hypotheses for sex ratio variation were evaluated. This study failed to support the Female Condition, First Cohort Advantage, or Resource Competition hypotheses. There was limited support for a Disturbance hypothesis. This

hypothesis predicts that if there is a skew in the adult sex ratio, there should be selection for females to assess the current adult sex ratio and produce the scarce sex. During 1993, the adult population was significantly biased towards males, and females, on average, produced more daughters.

To date, the studies of the reproductive strategies of female opossums have examined facultative sex ratio variation. In nature, it is likely that several factors affect a female's reproductive decisions. In addition to the sex ratio of offspring, the litter size is also an important factor affecting a female's fitness. If sons and daughters do not cost the same to produce, investing differentially in one sex will alter both the sex ratio and the number of offspring produced. This study provides an example of the need to consider the relationship between reproductive effort and sex allocation when examining female reproductive strategies.

The third objective of this study was to compare sexually dimorphic characters between the sexes and among males. In this study, male opossums were significantly larger and had larger canine teeth than females. Male canine lengths were significantly larger than predicted based on body size differences alone, although this was not the case for females. Canine length varied isometrically with body size in females. In addition to larger body and canine sizes, male Virginia opossums possess a sternal gland that exudes a musky odor and stains the chest a yellow/orange color. In this study, the sternal stain first appeared in males when they were five months old. The sternal stain increased isometrically as male body size increased then declined rapidly prior to the animal's death. The results of this study suggest that these sexually dimorphic traits may be products of sexual selection, and males with larger body and canine sizes may be more successful in competing with other males to acquire mates. In addition, these dimorphic characters may also serve as indicators of a male's dominance status, age, or condition.

<u>Future Studies</u>

Most of the published information of the Virginia opossum prior to this study was based on studies in North America. This study demonstrates that there may be significant differences in morphology, population structure, and reproduction at the southern limit of this species' range. To date, there is very little information for this species throughout Central America. There is a need for further studies on the basic natural history, population biology, morphology, and reproduction for this species in Central America before we can fully understand the geographic variation in the life history of this animal.

The results from the examination of female reproductive strategies suggest that studies are needed to further evaluate the energetic tradeoff between numbers and sex of offspring, and to consider the relationship between life-history and sex allocation theory when evaluating individual reproductive strategies. In addition, the Disturbance hypothesis proposed by Werren and Charnov (1978) warrants further examination. An experimental removal of one sex from the adult population should be attempted to determine the reproductive response of females.

Finally, few studies have examined the reproductive strategies of male opossums and the true function of the sternal glands is poorly understood. The different mating strategies of males of different age classes is not clear, especially in populations with varying numbers of cohorts, such as those found in North and Central America. Comparative studies would aid in the understanding of the different selection pressures and the resulting reproductive strategies of the Virginia opossum across its range.

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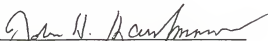Sealander, J. A. 1979. A guide to Arkansas mammals. Conway: River Road Press.

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BIOGRAPHICAL SKETCH

Monica Marquez was born and raised in El Paso, Texas. She attended the University of Texas at El Paso for two years, then transferred and completed her Bachelor of Science degree in Zoology at Texas A&M University in 1983. She received a Master of Science in Wildlife Science in 1988 from Oregon State University, where she studied the leadership behavior and foraging strategies of Roosevelt elk. She then traveled across the country, stopping to study bison in the Badlands National Park, en route to the University of Florida where she completed her Ph.D. in Zoology in 1994. For her dissertation, Monica examined life history variation and reproductive strategies of the Virginia opossum in Costa Rica. Monica plans to pursue a postdoctoral research position examining the biodiversity of mammals on native American Indian lands in Nevada. She plans to teach and conduct research in the areas of behavioral ecology and conservation.
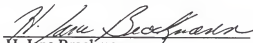
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John H. Kaufmann, Chairman
Professor of Zoology

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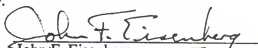Associate Scientist of Forest
Resources and Conservation

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H. Jane Brockmann
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Richard A. Kiltie
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

December, 1994

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